

THESIS

PRESENTED TO THE

UNIVERSITY OF EDINBURGH

FOR

THE DEGREE OF DOCTOR OF MEDICINE

BY

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OBSERVATIONS ON THE VASCULAR SYSTEM

OF

A FOETAL FEMALE BALAENOPTERA PHYSALUS



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## INTRODUCTION

The study of the structure of whales presents difficulties that are absent from the study of land mammals. Their size makes anatomical dissection, in the accepted sense, almost impossible, and, further, fresh material is difficult to obtain for decomposition, especially of the viscera, begins soon after death; preservation of the tissues when it is attempted is thus usually unsatisfactory and foetal material is seldom good. It is for these reasons that comparatively little systematic work has been done on the soft parts of whales. It was with pleasure, therefore, at the instigation of Dr. G. L. Streeter, Director of the Carnegie Institute of Embryology, Baltimore, that I undertook the dissection of the vascular system of a foetal female whale (*Balaenoptera physalus*) which had been placed at the disposal of the Institute by Dr. E. M. K. Geiling.\* He had obtained it during an expedition to the whaling station of the American Pacific Whaling Company at Rose Harbour, Queen Charlotte Islands, B.C., Canada, in July 1935. It was 143 cm. in total length, and therefore /

\* The greater part of this work was carried out in Baltimore, Md., U.S.A., while candidate held a Rockefeller Fellowship awarded by the British Medical Research Council; the work was completed in the Anatomy Department, University of Edinburgh.



Fig. 1.

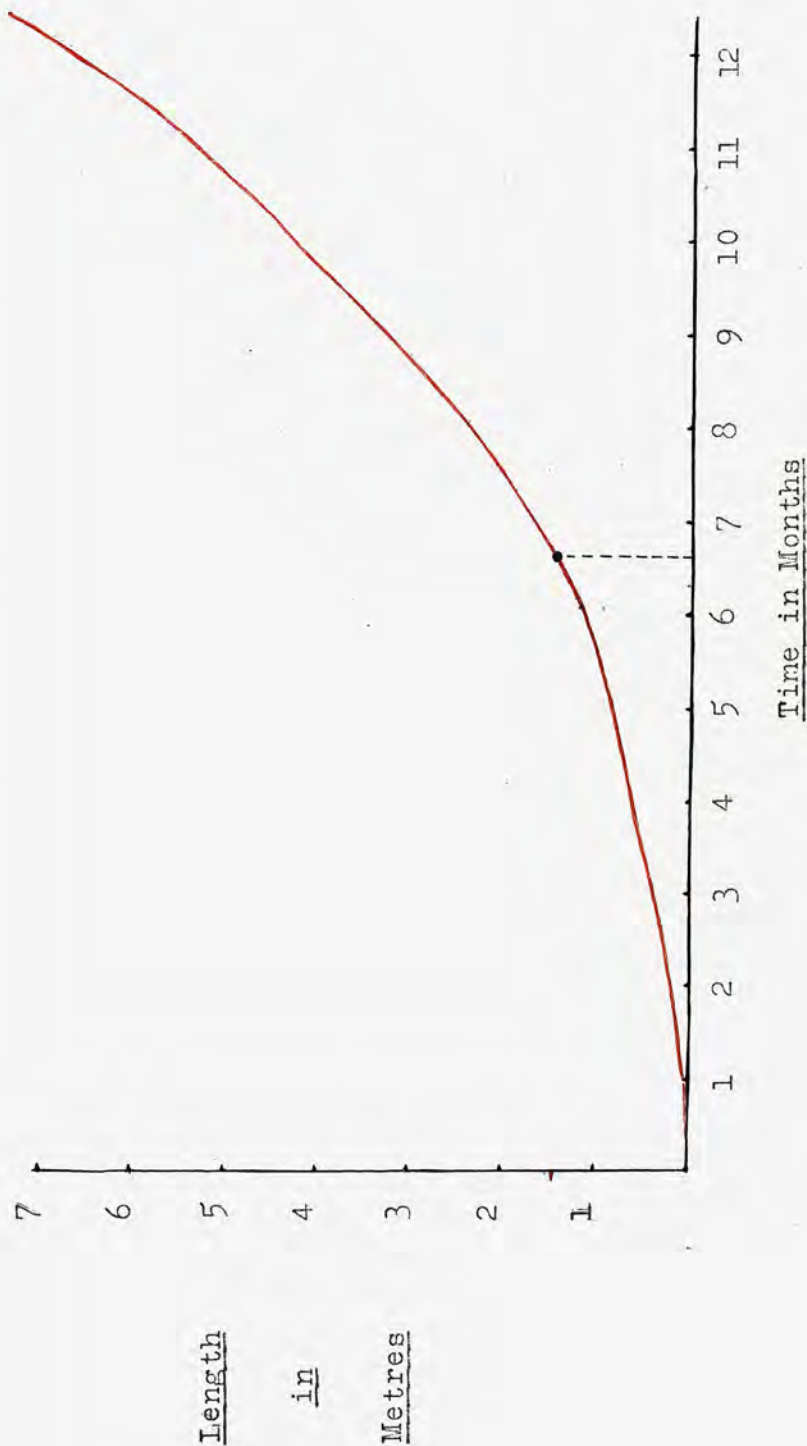


Fig. 1. Mean curve of growth during gestation in Finback Whales. From this curve the age of the 143 cm. foetus is calculated to be about six and a half months.

(Adapted from Fig. 150, Mackintosh and Wheeler, 1929, Southern Blue and Fin Whales. Discovery Reports, Vol. 1)

therefore almost certainly in the second half of the gestation period (Fig. 1). It had been divided into three pieces and stored in 10% formalin; no injection of the vascular system had been made, but the general preservation of the tissues was fairly good.

The study of the vascular system was suggested to me because of the absence of a systematic account of it and the divergence of opinion there is on the structure and significance of the retia mirabilia which are characteristic in the marine mammals. As my work on the foetus progressed it became evident that I should have also to examine adult whales, for though it was recognised that the general vascular pattern of the mid-term foetus was practically certain to be that of the adult, the arrangement of some of the vessels was so different from the usual arrangement in mammals that verification in the adult was necessary to make sure that the condition in the foetus was not merely a phase in development. It was then discovered that some of the specialised features of the adult system are poorly developed in a foetus of this size; this is specially so of the retia mirabilia. It has been necessary therefore to introduce some data obtained from the adult whales and other foetal material that I had access to, but I have attempted to hold to my original purpose and provide a systematic account of the vascular system of a foetal female finback whale.

## MATERIAL.

As is stated in the introduction the basis of this study is a foetal female finback 143 cm. long. Dr Geiling, in addition to providing this specimen, also placed at my disposal a foetal male finback 46 cm. long, and the brain and cervical spinal cord with the meninges and surrounding retial tissue of an adult finback. It was extremely unfortunate that the male foetus permitted an examination only of its external anatomy and larger vessels as most of the internal organs had undergone decomposition. I am greatly indebted to Dr Geiling for this material and also for his constant and stimulating interest in my work.

### Description of the Material.

When it became necessary for me to have access to adult material Dr Geiling and I journeyed to Rose Harbour, Queen Charlotte Island, B.C., where we became the guests of the American Pacific Whaling Company. To the Company and their representatives on the station I should like to extend my sincere thanks, not only for their hospitality and courtesy, but also for their help in the furtherance of my task. While on the station I was able to make many observations, some of which are incorporated in this work, and to collect specimens/

specimens for histological study from Sperm (*Physeter macrocephalus*), humpback (*Megaptera nodosa*) and finback (*Balaenoptera physalus*) whales. I was also fortunate enough to obtain two foetal female finbacks, 86 and 65 cm. long respectively. These specimens had been collected before my arrival at the station but had been placed entire in 10% formalin soon after their discovery. After the measurements and photographs of these fetuses had been made, the internal organs were dissected out and preserved for study at a later date.

During the whole course of the work Dr G.L. Streeter gave me much helpful advice and criticism and to him I extend my warmest thanks. To the members and technical staff of the Carnegie Institute of Embryology I am much indebted for their help, and my special thanks are due to Mr J.F. Didusch who spared no pains in the preparation of the drawings. These drawings were often made under great difficulty as there had been no injection of the vascular system and the patience and skill of the artist in interpreting the dissections were necessary to make them possible.

#### Measurements.

The measurements of the four foetal finbacks, one male and three female, are given in Table 1. I have included/



T A B L E 1.

DATA REGARDING FOUR FOETAL FINBACKS (BALAENOPTERA PHYSALUS)  
CAPTURED OFF THE QUEEN CHARLOTTE ISLANDS BY THE AMERICAN PACIFIC WHALING COMPANY

Series Number . . . . .	1.		2.		3.		4.	
Length of Mother . . . . .	73 feet.		68 feet.		62 feet.		58 feet.	
Date of Capture . . . . .	28th July, 1935.		11th May, 1936.		25th June, 1936.		7th June, 1935.	
Sex of Foetus . . . . .	Female		Female.		Female		Male	
Measurements of Foetus	mm.	% total	mm.	% total	mm.	% total	mm.	% total
Total length, snout to notch of flukes.	1430	.	860		650		467	
Tip of snout to blow-hole.	252	17.6	125	14.5	100	15.3	70	15.0
Tip of snout to eye.	310	21.7	170	19.8	140	21.5	86	18.4
Tip of snouth to mid-axilla.	500	35.0	280	32.6	230	35.4	140	30.0
Tip of snout to umbilicus.	770	53.8	400	46.5	300	46.1	197	42.2
Tip of snout to clitoris or penis.	930	65.0	510	59.3	380	58.5	250	53.5
Tip of snout to anus.	1010	70.6	550	64.0	400	61.5	285	61.0
Tip of snout to dorsal fin.	1170	81.8	600	69.8	480	77.2	320	68.5
Length of attached border of dorsal fin.	79	5.5	36	4.2	27	4.1	25	5.4
Greatest height of dorsal fin.	42	2.9	20	2.3	17	2.6	13	2.8
Notch of flukes to umbilicus.	710	49.7	430	50.0	300	46.1	268	57.4
Transverse width of flukes.	475	33.2	190	22.1	155	23.8	111	38.8
Anus to clitoris or penis.	42	2.9	30	3.5	20	3.1	15	3.2
Anus to umbilicus.	250	17.5	140	14.3	110	16.9	87	18.6
Diameter of umbilicus.	39	2.7	28	3.2	18	2.8	13	2.8
Depth of trunk at shoulder	235	16.4	190	22.1	130	20.0	114	24.4
Circumference of trunk at shoulder.	700	48.9	490	57.0	370	56.8	317	67.9
Depth of trunk at umbilicus.	220	15.4	160	18.6	130	20.0	107	22.9
Circumference of trunk at umbilicus.	610	42.7	430	50.0	350	55.5	273	58.5
Depth of trunk at anus.	163	11.4	100	11.6	80	12.3	52	11.1
Circumference of trunk at anus.	435	30.4	255	29.6	210	32.3	160	34.2
Length of anterior border of flipper.	198	13.8	115	13.4	90	13.8	66	14.1
Greatest breadth of flipper	49	3.4	30	3.5	25	3.8	20	4.3
Greatest thickness of flipper.	10	0.7	7	0.8	6	0.9	3	0.6

included the measurements of fetuses Nos. 2, 3 and 4, because although no systematic dissection of the vascular system was made on them, they were repeatedly used for confirming my observations. The largest of the fetuses (C 544 of the Carnegie collection and No. 1 of this series) had been cut into three parts prior to its immersion in 10% formalin, and the measurements of it were made after the parts had been placed in positions as closely approximating the original as could be determined. All measurements, unless otherwise stated, represent linear distances between the named points and were made by external calipers. In addition to the actual measurements the percentage proportion of each measurement to the total length is given.

I should like to stress the fact that none of the measurements were made on fresh fetuses but were made on specimens after they had been in 10% formalin for periods varying from two weeks to four months. In addition, the distortion that resulted from the sectioning of fetus No. 1 into three pieces was such as still further to detract from the value of its measurements. Fetuses Nos. 2, 3 and 4 had all been preserved in containers that were too small for them so that they were curved in their long axes and the measurements were made after they had been forcibly straightened./

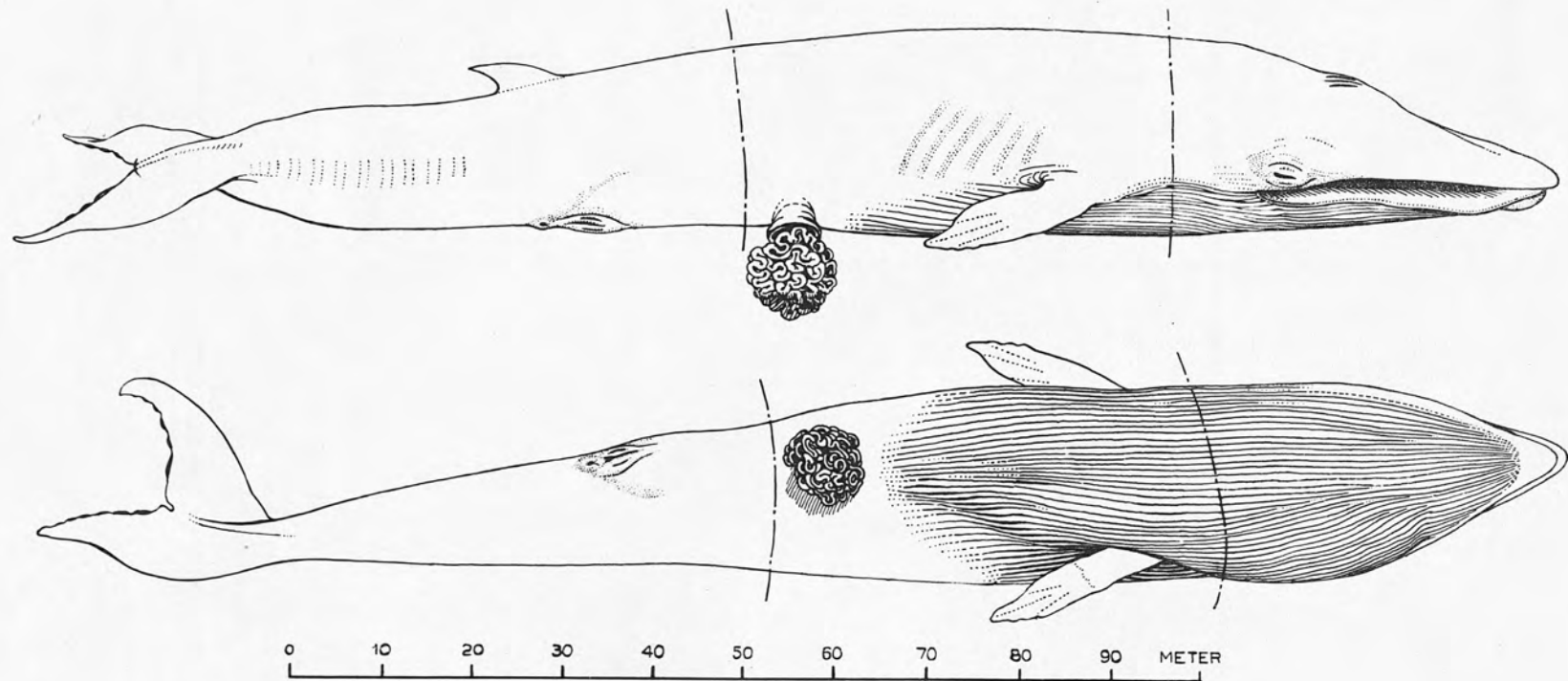


Fig. 2. Foetus No. 1 (1430 mm.). Side and ventral views. Drawings were made from photographs taken after three pieces of foetus had been placed together. The interrupted lines indicate plane of section.



Fig. 3. Foetus No. 2. (860 mm.).  
 Photograph taken at Rose Harbour  
 prior to removal of viscera.



Fig. 4. Foetus No. 3. (650 mm.).  
 Photograph taken at Rose Harbour  
 prior to removal of viscera.



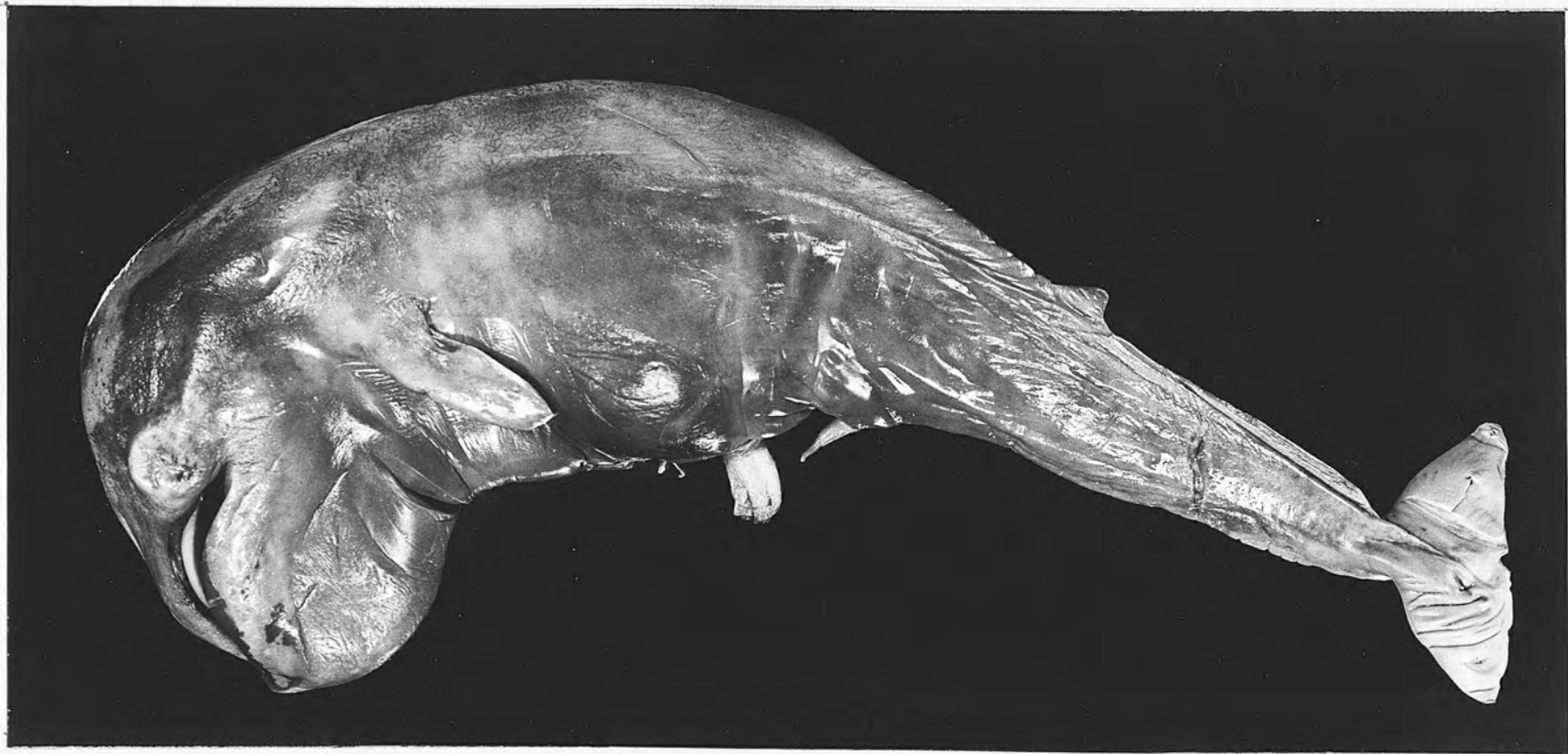


Fig. 5. Foetus No. 4 (467 mm.) x  $\frac{1}{2}$ . Left side.

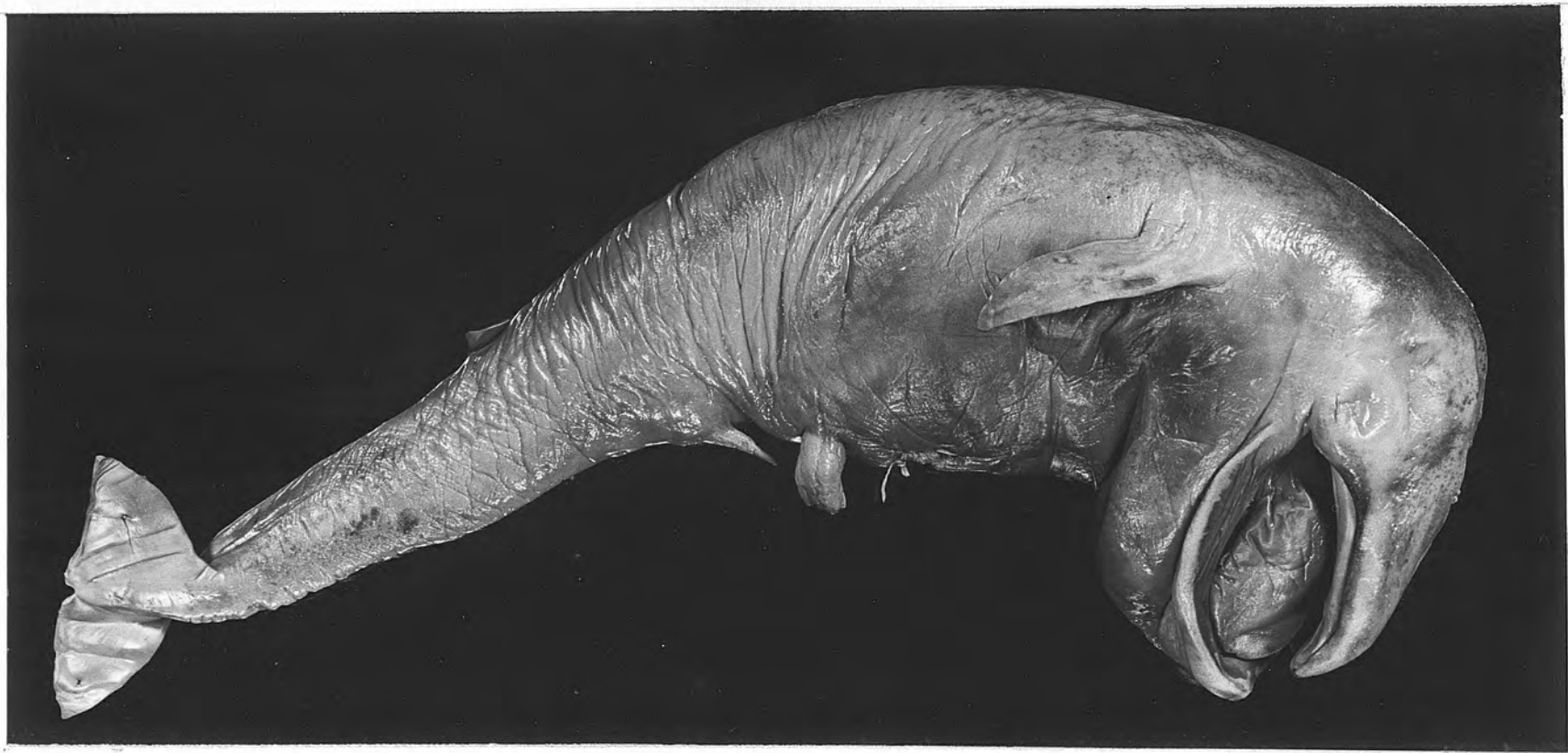


Fig. 6. Foetus No. 4 (467 mm.) x  $\frac{1}{2}$ . Right side.

straightened. The effect of these factors on the form of the specimens is very considerable and the data in Table 1 must only be interpreted in the light of them.

FOETUS NO.1. (Total length = 1430 mm.)

Age. The age of this foetus, as estimated from the work of Mackintosh and Wheeler (1929), is about six and a half months, i.e. the commencement of the second half of gestation (Fig.1).

Colouration. There has been a certain amount of discolouration caused by the 10% formalin in which the foetus had been immersed for about 9 weeks prior to work being commenced on it. It is, on the whole, of a buff colour and is slightly darker on the back than on the sides or ventral surface.

Scattered over the snout - especially in the region of the blow holes - are black patches, and around the oral orifice there are irregular black strips of desquamating epithelium, signifying the epidermal nature of the pigment.

This colouration of the foetus is in marked contrast to the colour of the living or newly killed adult finback where the back and sides are of a bluish-grey hue and the ventral surface white. The/medial/

medial surface of the flippers and the under surface of the flukes, except at the anterior and posterior margins, are also light in colour. True (1904) has described the rapidity with which the colour of a whale changes when the animal is killed and drawn out of the water, and states that eventually the entire pigmented area becomes black, the process being accelerated by the action of the sun. If the mere exposure to the air causes such a change in the adult colouration, the effect upon the colouration of a foetus that results from immersion in formalin can also be taken to be very appreciable.

Hairs. The hairs on the snout are arranged in two parallel rows, an outer row about 20 mm. from the free margin of the lip, and an inner about 35 mm. from the margin. In the outer row on the left side there are 5 hairs, in the inner row 4 hairs, and on the right side there are 6 and 4 hairs respectively in the rows. The most anterior of the hairs is about 120 mm. from the tip of the snout while the most posterior is about 60 mm. in front of the eye.

The skin of the lower jaw is redundant and oedematous, and this makes the hair follicles difficult to identify. Commencing about 20 mm. in front of the angle of the mandible is a row of hairs that are situated about 15 mm. from the free margin of the lip and/

and about 40 mm. from one another. These are easily identified posteriorly, but towards the tip of the snout they are seen only with difficulty even with the aid of a hand-lens.

Body Outline. The body outline was adjudged after the three sections were set on a table in as nearly their proper relationship to one another as could be judged. (Fig.2).

From its tip, the rostrum extends backwards and upwards at an angle of twenty degrees to the horizontal and this slope reaches as far back as the slight hollow which lies immediately in front of the eyes and contains the blow-holes. From there back there is a slight convexity which extends as far as the dorsal fin; from there there is a gentle slope downwards and backwards to the flukes. No definite conclusions can be reached regarding the contour of the ventral surface as the soft tissues of that region are flaccid and redundant so that there is a complete flattening of the surface when the foetus is placed on it. At the posterior end, however, the ventral body outline ascends so that the flukes are placed on a plane slightly nearer the dorsal than the ventral surface. When the posterior portion is laid on its side the labium majus forms a slight convexity immediately in front of the anus.

Head./

Head. As stated above, the anterior cut had been made immediately behind the occipital condyles so that the head forms a section by itself. There was some laceration of the tissues of the ventral pouch, and the body of the mandible had been cleft on the left side. The rostrum is convex from side to side and on its anterior part there is a medial sagittal crest which expands out immediately in front of the blow-holes to become continuous with the elevation on either side of these apertures. The blow-holes are cranio-caudal slits about 40 mm. long with their anterior ends about 7 mm. apart and their posterior ends about 23 mm. apart. The lips of the blow-holes could be forcibly separated to admit the tip of one finger.

The eyes are situated just behind the level of the blow-holes and immediately above the posterior end of the oral orifice. The bony orbital margin can be felt above, in front and behind, and it has a maximum diameter of about 40 mm.; the lower lip expands posteriorly to complete the orbital boundary below. The separation of the eye-lids is not yet complete and the horizontal cleft which is only about 16 mm. long is situated at the junction of the upper four-fifths and lower fifth of the globe. The external auditory meatus is extremely small and as corroborated by dissection and exposure of the cartilage, is placed 80 mm./



80 mm. behind and 30 mm. above the level of the centre of the eye-ball. The line of closure of the lips is nearly horizontal with a slight upward convexity; the lower jaw overlaps the upper except at the extreme tip of the snout where there is the reverse relationship.

Extending throughout the greater part of the upper jaw there are the two grooves, an inner dental, and an outer labial. Whereas the labial groove extends the full extent of the upper jaw from the naso-vomerine organ in front to where the jaw sweeps medial to the temporal muscle posteriorly, the dental groove stops short of the tip of the snout by about 40 mm. and only extends to within about 50 mm. of the eye. Both in front and behind, the dental groove gradually shallows, so that what is to form the upper lip (Schulte, 1916) gradually merges with the palate. This ridge between the two grooves is of a white colour and is in marked contrast to the colour of the palate and the outer ridge. No tooth germs could be observed either in the course of the ordinary dissection or in microscopic sections. The palate is long in comparison with its width; it reaches its maximum width about four-fifths of the way back. The intermandibular tissue is exceedingly loose and redundant and on its external surface there are the typical ventral grooves; the medial grooves are the largest/

largest and reach almost to the umbilicus, and the most lateral are the shortest and only reach the flipper.

The Flipper. The axis of the flipper is at angle of about  $20^{\circ}$  to the horizontal. Both the anterior and posterior borders are convex, - the anterior border slightly, the posterior markedly so. The posterior border is reduced to a flaccid edge but the anterior border is firm and rounded.

The umbilicus is a rounded orifice with a general diameter of 40 mm. Through the orifice there projects a coil of the small intestine - the result of a trauma after the removal of the foetus from the uterus.

The genital orifice is about 31 mm. long and is guarded on either side by a well developed labium majus. Anteriorly the labia converge, but posteriorly they become continuous with the skin on either side of the anus. About two-thirds of the way back each labium has a punctate orifice barely wide enough to admit a match-stick. Hidden by the labia and only seen when they are forcibly parted is the clitoris about 15 mm. from the surface; the urethral meatus is too contracted to be visible.

The anus is situated on the apex of a rounded convexity and is just large enough to admit a match stick.

The flukes are triangular and flattened. The posterior/



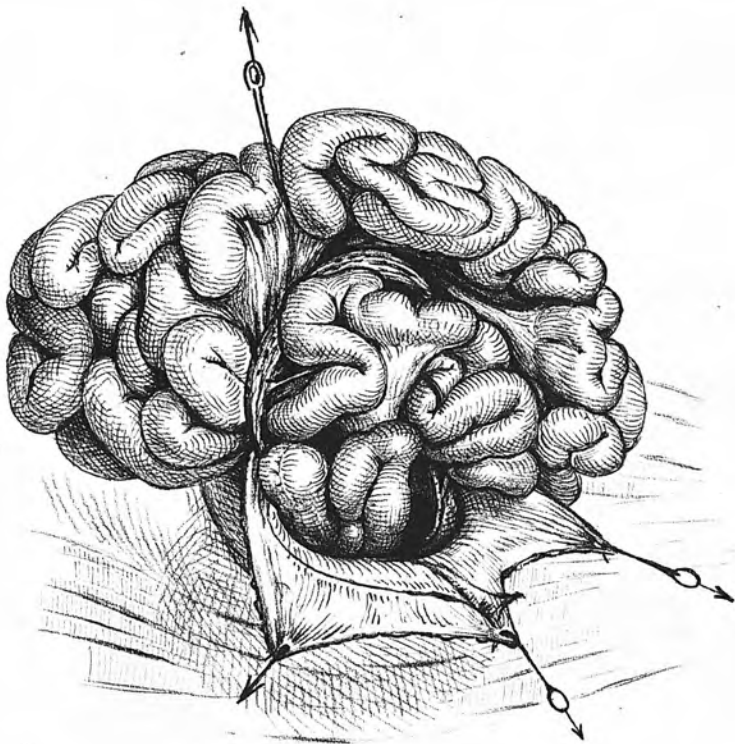


Fig. 7 . Coil of small intestine which projected through umbilicus; this is the result of trauma after death.

posterior border is concave and extremely thin, while the anterior is thickened and convex. In the mid-line there is a notch 5 mm. deep, to which a crest from the dorsal surface of the trunk extends; the crest from the ventral surface does not quite reach as far as the notch.

The dorsal fin lies just behind the level of the anus. It is triangular in shape and its antero-superior border of 107 mm. is the longest; its posterior border is slightly concave.

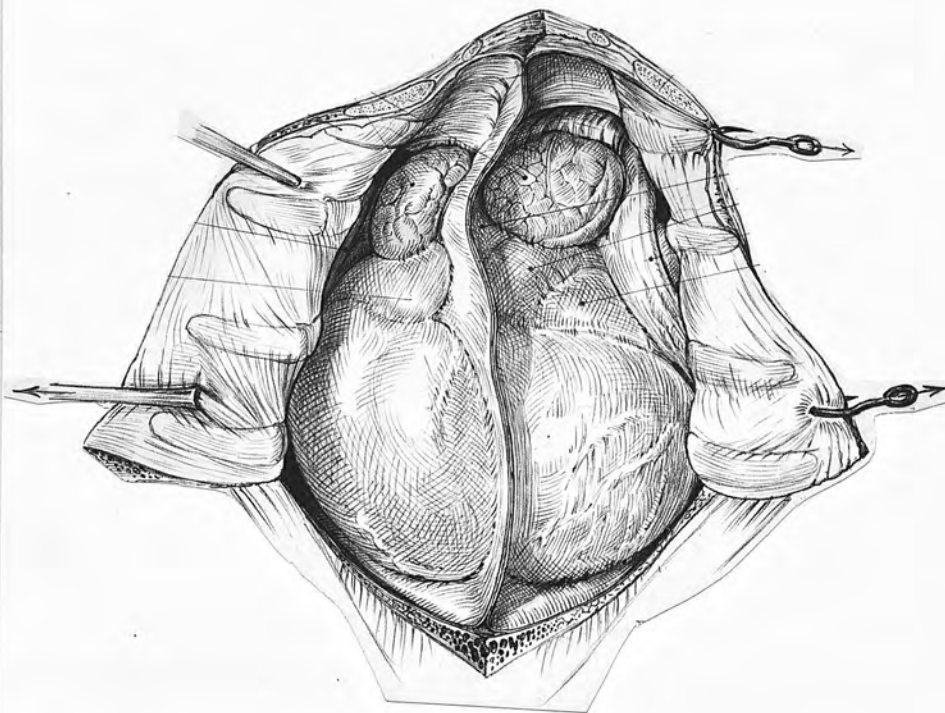
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THE PERICARDIUM.

The pericardium has the usual form, - a fibro-serous sac that invests the heart and the adjacent parts of the great vessels. It lies behind the part of the chest wall that extends from the first to the fourth costal cartilages. The outer fibrous layer, which is extremely loose and redundant owing to the shrinkage of the heart, is conical in form; the base rests on the diaphragm and the apex extends onto and embraces the aorta and the pulmonary artery. The peripheral part of the base is easily separated from the diaphragm, being attached to it only by loose areolar tissue, whereas the central part is fused. The fibrous pericardium is prolonged forwards onto the ventral surfaces of the pulmonary artery and the arch of the aorta, while dorsally it blends with the tunica adventitia of the right and left pulmonary arteries. On the basal surface of the heart the pericardium and the wall of the left atrium are fused over a large area (see left atrium), the area interposita (of His). The single pulmonary vein pierces the pericardium in that area and there is therefore an absence of the oblique sinus. The transverse sinus is sufficiently large to admit one finger and has the usual relationship to the great vessels.

It/

It is of interest to note that there is no bare area of the heart as the right and left mediastinal pleurae meet in the mid-ventral line of the pericardium and from there are prolonged ventrally as a fold to the thoracic wall.



Legends.

Fig. 8. Interior of thorax after reflection of ventral wall.

## THE HEART.

The following description of the heart is based primarily on the heart of foetus No.1, and where measurements are given and if not otherwise stated it is to that specimen they refer. The hearts of foetuses Nos. 2 and 3, were, however, in a much better state of preservation, and much use was made of them in compiling the description.

### GENERAL SHAPE AND POSITION.

When the atria and ventricles are distended the heart has the shape of a flattened cone with two large surfaces - costal and diaphragmatic - and a much smaller basal surface (Fig. 9a and b). Each atrium plays an almost equal part in the formation of the basal surface, a departure from the condition in the human; the surface is elongated in the transverse plane and looks almost directly dorsally. The costal surface is convex from side to side and looks in a ventral and cranial direction; it lies behind the chest wall from the second to the fourth costal element. The diaphragmatic surface is flattened and looks in a caudal direction.

The relative shortness of the cervical and anterior/

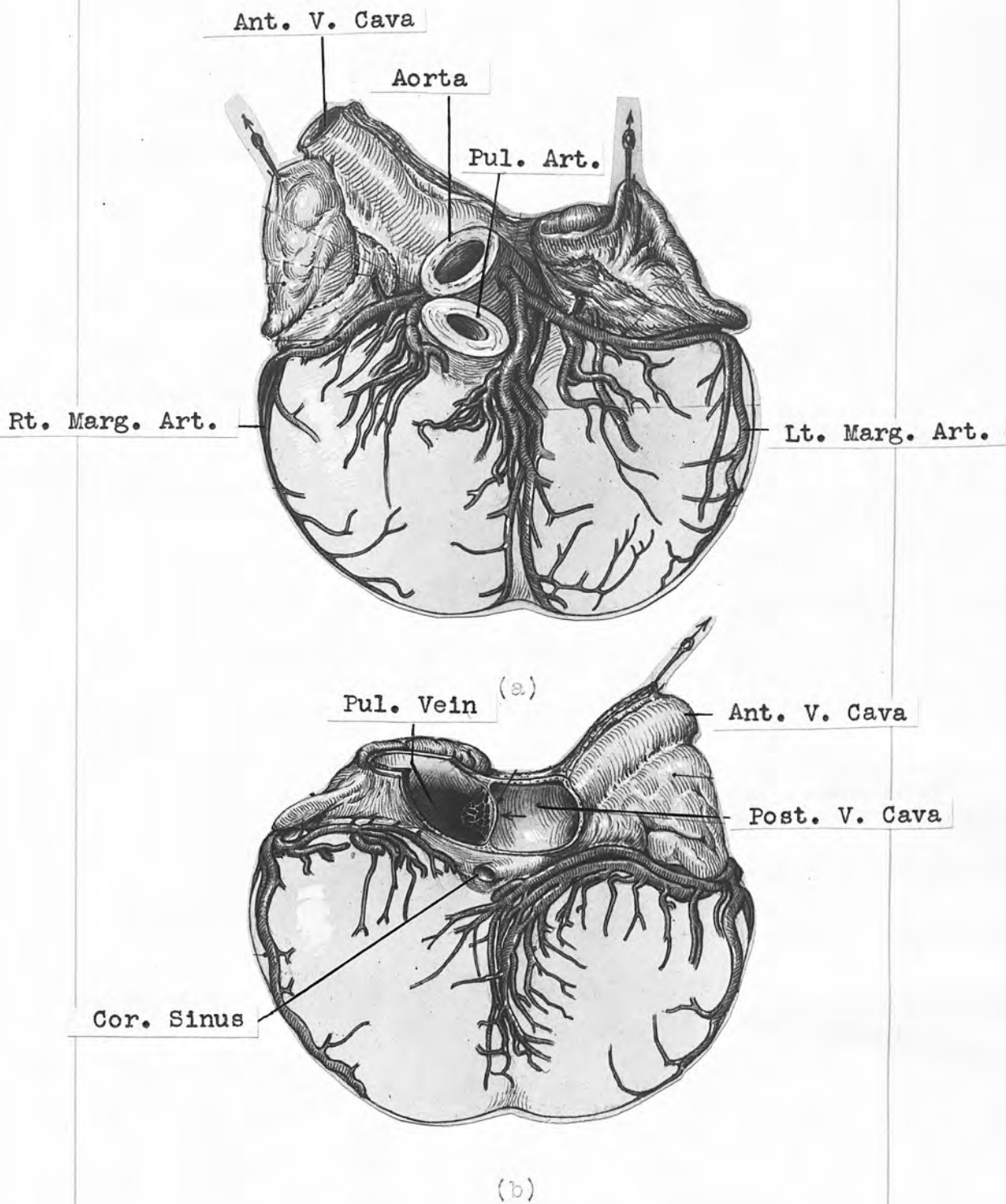


Fig. 9. The ventral (a) and the diaphragmatic and basal (b) surfaces of the heart. The valve of the foramen ovale is shown in (b).



anterior thoracic regions in Cetacea is well known; it is often associated with the fusion of a variable number of cervical vertebrae. Howell (1930) ascribes the shortening to the necessity of forming the "fusi-form shaped" body that is best adapted for passage through the water. Müller (1898), moreover, has pointed out that the shortening of the anterior thoracic region is in no wise limited to the Cetacea, but that it is a feature of all mammals that have become adapted to marine life, and that it is most marked in those that show the greatest marine adaptation. Müller believes that this process has influenced the position of the heart in that it has caused its long axis to assume an almost vertical position. Slijper (1936), in addition to observations on his own specimens, has analysed the literature regarding the position of the heart in Cetacea and has concluded that in the Odontoceti the heart has a horizontal position - a view diametrically opposed to that of Müller. In a 105 mm. foetal Balaenoptera acutorostrata, the only Mysticetus that Slijper examined, he found that the long axis of the heart was in a more or less vertical position. This finding is in agreement with the views depicted for other Balaenoptera by Müller (1898 - Balaenoptera musculus L.) Marschner (1901 - Balaenoptera physalus), Schulte (1916 - Balaenoptera borealis) and Ommanney (1932a - Balaenoptera/

*Balaenoptera physalus*). In foetus No.1 of my own series, the long axis of the heart formed an angle of about  $75^{\circ}$  with the vertebral column, but the position was probably altered to some extent by the fixation and prefixation treatment. In the other three foetuses - where however extrinsic factors may also have caused some change - the long axis of the hearts also had a more or less vertical position. An attempt was made to establish the direction of the heart axis in adult finbacks and sperms, but accurately to define the position of the heart was impossible, partly on account of the displacement that occurs during the opening of the thoracic cavity and partly on account of the size, weight and softness of the organ. It may be deduced from the work of Lenkeit (1927), however, that the heart axis in the adult finback is essentially similar to that in the foetuses.

On account of the vertical position of the heart, the length of the chest wall with which it is in relation, is relatively small, as the apex reaches only as far as the level of the fourth intercostal space - or allowing for contraction of the heart by the fixatives, the fifth rib or space - and the anterior end is well within the inlet of the thorax. This last relationship is in marked contrast to that which has been described in the adult *Phocaena phocaena* by/



by Slijper (1936), where the heart base - the heart being horizontal - actually lies outside the inlet of the thorax during expiration and at the level of the inlet during inspiration.

The heart is broad from side to side and short in length and bears a very close resemblance to the heart of the foetal elephant described by Eales (1929).

The greatest width of the heart, 114 mm., is at the base of the ventricles (61 mm. being to the left and 53 mm. to the right of the mid-line) while the greatest length is 66 mm. This comparative shortening of the heart in its long axis has frequently been observed and commented on in Cetacea. Müller (1898) has correlated the form with the shortening of the ventral wall of the thorax. In view of the fact that it is the base of the heart that lies in the true long axis of the body, I suggest that any shortening of the thoracic wall will reveal itself primarily in a diminution in the cranio-caudal length of its basal surface, and only secondarily in a shortening of the heart in its own long axis. This is in keeping with the findings in the specimen under discussion, where the atria are shortened in the cranio-caudal direction and have consequently elongated transversely.

Zimmermann (1930), however, contends that the shape of the heart is dependent on the work it has to perform, /

perform, namely a heart which has to produce a large blood pressure (bird, adult man) has a conical shape, whereas a heart which is associated with a low blood pressure (new-born child, fish) has a spherical form. In support of this assumption Gschwend (1931) states that the domestic pig has a more spherical heart than the more active wild pig, and Waldmeier (1928) has corroborated this in his observations on wild and tame deer and on race and work horses. On the other hand it has been pointed out, Ackerknecht (1925), and it is of course indisputable, that the heart assumes a spherical form in the hypertrophy of overuse.

The ventral part of the atrio-ventricular groove is hidden by the large auricles which overhang the anterior parts of the ventricles. The ventral inter-ventricular groove lies 7 mm. to the left of the median plane, with which it is parallel; it is deepest at the base of the ventricles and gradually becomes shallower towards the inter-apical depression. The posterior interventricular groove, which is also situated more towards the left side, is about 5 mm. deep in its whole length. Both grooves are bridged by the epicardium and contain fat and the larger branches of the coronary arteries and veins. There are no superficial ventricular muscle layers crossing from one ventricle to the other - as is found in longer, more pointed/

Ventral interventricular groove

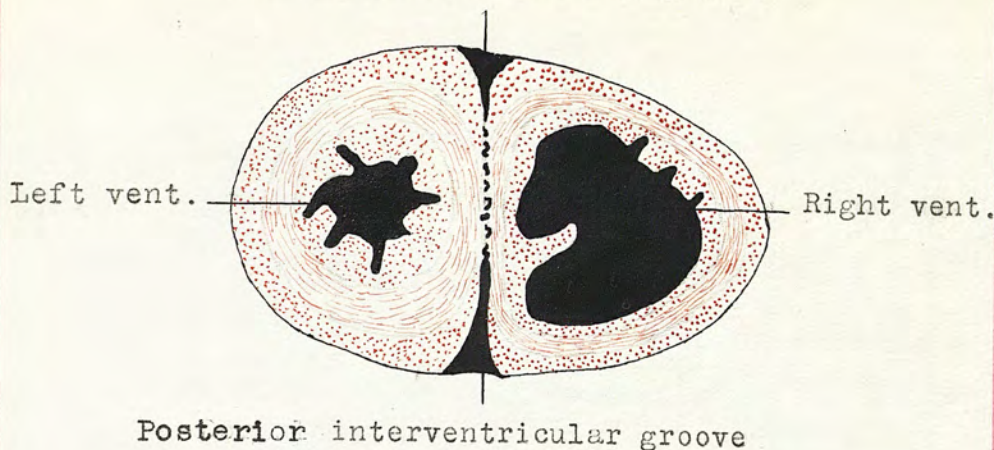


Fig. 10. A diagram of a transverse section through the ventricles.

pointed hearts, for example, in the human subject and the sheep, except across the floor of the interapical depression; here, below the cavities of the ventricles, there is a superficial muscle band passing obliquely to the left from the anterior surface of the right ventricle to the posterior surface of the left ventricle, but otherwise all the superficial layers of the myocardium turn into the interventricular grooves. This suggests that there is an independence of the ventricular walls which is not usual, or at least does not occur in the human subject, the Primates generally, the sheep, the ox, or the dog. A horizontal section through the middle of the ventricles, confirms the independence of structure of the ventricles, for it is there seen that each ventricular system of the myocardium completes itself in the septum without admixture/



admixture with the other system and that between the two ventricular systems there is a septum of loose fibrous tissue (Fig. 10). This separation of the ventricles explains the bifid apex of the Cetacean heart; it reaches its full expression in the dugong in which the ventricles are almost completely separated (Owen, 1868). Each ventricular muscle system, as seen when examined with a lens (x 8), consists of a central mass of more circular fibres and superficial and deep layers of oblique and longitudinal fibres; the superficial longitudinal fibres are not continued through the septum from the anterior to the posterior surface (Fig. 10 ).

The Atria form the base of the heart and as seen from the dorsal side are separated from the base of the ventricles by a deep atrio-ventricular groove in which lie the coronary sinus and the dorsal parts of the coronary arteries. The bottom of the groove is bridged by epicardium but I could not discover any muscular bridges between the atria and the ventricles; such surface connections were described by Kent (1893) in ungulates. The atrial chambers are elongated transversely and shortened anter<sup>^</sup>-posteriorly; the right atrium is not elongated in the caval axis as in most mammals. The atria are adherent to the pericardium over a wide area - the dorsal mesocardium or area/

area interposita of His; in the mesocardium lies the pulmonary vein, formed by a large single right vein and two smaller left veins. The area of adhesion does not include the coronary sinus or the oblique vein of the left atrium (vein of Marshall) which are attached to the atrial wall by their own mesenteries. These arrangements correspond with the early developmental arrangements of the human heart, but the area interposita is relatively much larger.

Each atrium is continued ventrally into a large auricle; the two auricles embrace the bases of the aorta and pulmonary artery, their apices coming within 30 mm. of each other. The left auricle is the larger.

The Right Atrium. The area interposita extends over the posterior wall of the right atrium as far as the orifices of the anterior and posterior venae cavae which are included in it. There has therefore been a delayed separation of the dorsal mesocardium, at least when compared with the human heart.

The anterior vena cava is a thin-walled vessel 10 mm. in diameter. It enters the pericardium 15 mm. from the heart and joins the atrium abruptly, and as far as I could determine under magnification there is no extension of myocardium on to it; all round the junction there is a deep groove. The groove is continued from the ventral side of the cava on to its lateral/

lateral side and is then continued backwards on the dorsum of atrium to the right part of the posterior vena cava. The groove is the sulcus terminalis and it forms the right boundary of the area interposita; it lies along the dorsal edge of a rounded muscle band in the atrial wall which must be the crista terminalis. I could not detect the sino-atrial node in the usual position in the sulcus terminalis, but the circulus arteriosus - the arterial circle round the caval-atrial junction - is present.

The posterior vena cava is a thicker walled than the anterior cava and is 25 mm. in diameter.

The cavity of the atrium of Foetus No.2 was filled with post-mortem blood-clot. This was removed with the greatest possible care to discover, if possible, by the direction in which the blood-clot was set, the course through the chamber of the two streams of blood that enter it. The chamber was opened by a vertical incision from the right auricle dorsally to the crista terminalis and a horizontal incision just below the crista; the posterior end of the incision was afterwards carried into the posterior cava.

The crista terminalis is a well developed bundle, 6 mm. broad at its origin on the septum. There it is confluent with a powerful sphincteric bundle which encircles the right atrio-ventricular opening and both bundles/

bundles are continued laterally on the dorsal wall of the atrium as a large well defined torus intervenosus (Loweri), which projects ventrally between the anterior and posterior caval openings.

The orifice of the coronary sinus is 3 mm. wide and lies within the sphincter round the atrio-ventricular opening; there can be little doubt that the blood returned through it enters the right ventricle. The orifice of the sinus is unguarded, there being no remnants - either as trabeculae or folds - of the venous valves in its neighbourhood.

The orifice of the anterior cava lies dorsal to the anterior part of crista terminalis which leaves the septum and passes to the right in front of it. As the crista passes the right edge of the orifice a narrow band of muscle detaches itself from it and passes dorsal to the orifice, thus completing a muscular sphincter for the anterior cava. This is a more complete sphincteric mechanism than exists in the human heart or in the ox or the sheep. The wall of the atrium to the right of the anterior caval orifice is thin and highly trabeculated; along the trabeculae there are free cords stretching from the crista to its subsidiary bundle behind the caval orifice. This part of the atrium is distensible into a large diverticulum of the atrial chamber and is probably/



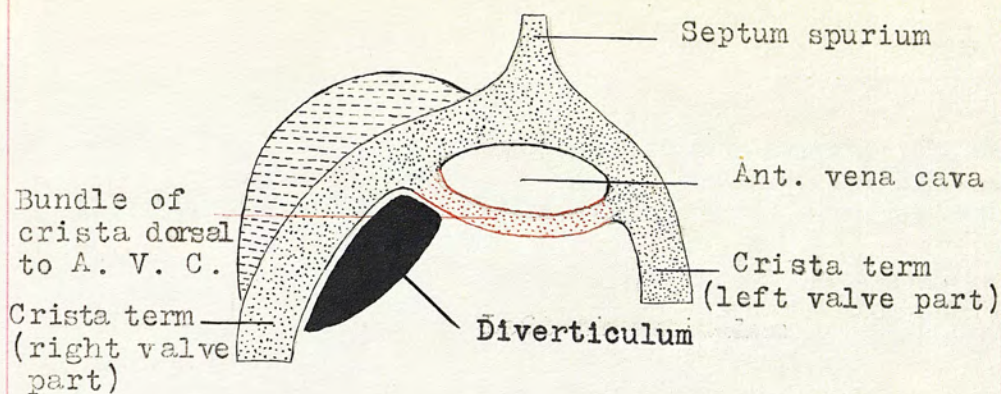


Fig. 11 A diagram to show the relations of the diverticulum.

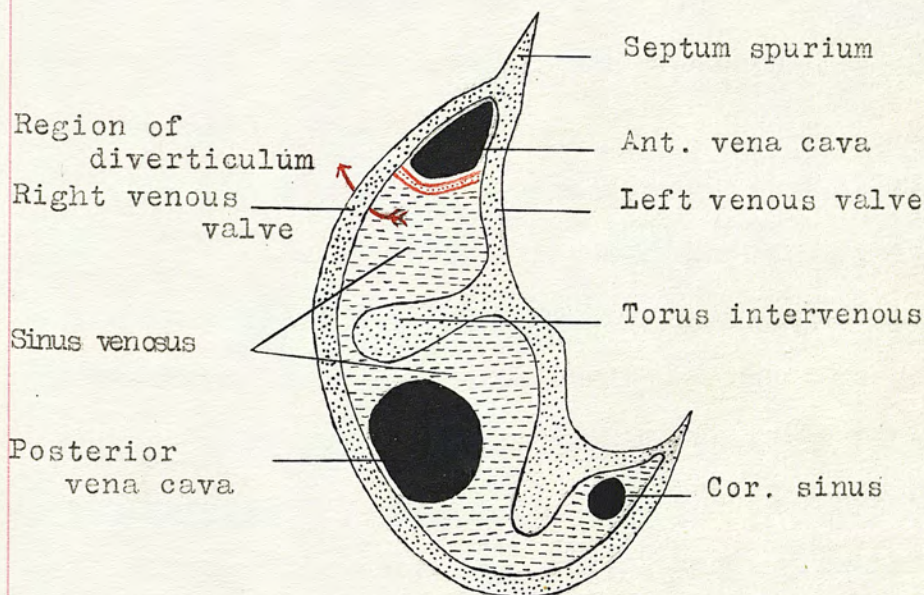


Fig. 12 Diagram of the interior of right atrium to show the division of the sinus opening. The part of the crista terminalis that passes dorsal to the anterior vena cava is in red.



probably functionally comparable to the spatium inter-septo-valvulare found in the hearts of monotremes and marsupials. It lies dorsal to the crista terminalis and is therefore part of the sinus region of the atrium, and the free trabeculae that cross it are probably the remnants of the right venous valve.

A reference to the development of these parts make this clear (fig.12 ); and further, the muscle band behind the anterior caval orifice represents a limbic fold of the same nature as the torus intervenosus and the fold which separates the posterior cava from the coronary sinus.

The right and left venous valves, represented by the crista terminalis on the right and left sides of the septum spurium - which passes from the crista on to the anterior wall of the atrium - thus form a very complete muscular sphincter for the anterior cava.

The posterior vena cava opens into the posterior part of the atrium and its orifice has a diameter of 25 mm. Immediately in front of the orifice there is an oval opening in the dorsal part of the atrial septum with a maximum diameter of 12 mm. As is characteristic of Cetacea the atrial septum is small and in its greater part it is formed by a duplication of endocardium. The pocket membrane (see left atrium) that projects into the left atrium is attached to the margin/

margin of the oval opening, which is therefore the foramen ovale. It is bounded in front by the torus intervenous, a prominent muscular ridge which passes from the septum to the right wall of the atrium, where it joins the crista terminalis; the torus also receives a slip from the sphincter of the right atrio-ventricular orifice. The position of the foramen ovale and its relation to the atrio-ventricular orifice make it certain that it is a true foramen secundum in the septum primum, and the absence of a limbus fossa ovalis indicates that in all probability a septum secundum is not formed in the Cetacean heart. The relations of the caval orifice and the foramen make it certain that at least the great part of the posterior caval blood passes through the foramen and its saccular extension into the left atrium. This was in every way borne out by the blood clot in the cavity of the right atrium.

In foetuses Nos. 1 and 2 there was a complete absence of the valve of the posterior vena cava, but in foetus No. 3 the lower part of the right venous valve was present and formed a caval valve and also a coronary sinus valve as strong and as well defined as in the human foetus. These structures have not been previously recorded in the Cetacean heart; this is probably due to their early and complete regression.

The auricle is relatively large and is covered on its inner surface by a complex network of muscoli pectinati, two of which pass between the medial and lateral walls. The thicker of the bridging columns has a diameter of about 3 mm., whereas the average height of the muscoli is about 2 mm.

The right atrium shows, therefore, the following features:-

- (1) A special sphincter for the anterior vena cava.
- (2) A special sinus diverticulum dorsal to the anterior vena cava.
- (3) A prominent torus intervenosus (Loweri).
- (4) A primitive foramen ovale mechanism (see left atrium).
- (5) A separation of the two streams of blood in it.
- (6) Absence of a septum secundum.
- (7) Early regression of the right venous valve.

The left atrium is a relatively thick-walled chamber, the average thickness of the wall being between 3 and 4 mm. The cavity of the chamber is divided into two parts, the atrium proper and the auricle, by a powerful muscular bundle encircling the cavity at the ventral edge of the ~~lateral~~ septum. This bundle joins the ventral part of a thick circular bundle that surrounds the atrio-ventricular opening.

The/

The walls of the auricle are richly trabeculated, but the walls of the atrium proper are smooth. The single pulmonary vein opens into the dorsum of the atrium in a deep recess; the orifice is unguarded by valvular folds but is surrounded by a powerful sphincteric muscle bundle - the crista terminalis sinistra. Immediately ventral to the crista is the dorsal part of the basal attachment of a thimble-shaped membranous sac which projects into the cavity of the left atrium from the septal wall; the distal part of the sac is freely fenestrated. The length of the extended sac from base to apex is 15 mm.; the base of the sac is oval and its maximum measurements of 12 mm. is directed dorsally and caudalwards. Two narrow muscular ridges pass between the ventral end of the septum and the adjacent muscular wall, but these are ill-adapted to exert any influence on the movements of the septum.

In foetus No. 1, as in the other specimens, the pulmonary veins unite to form a common trunk outside the pericardium. The common pulmonary vein, 20 mm. wide, is very short; its wall is extremely thin - much thinner than the walls of the more distal veins. It passes ventrally through the pericardium and the atrial wall which are adherent (area interposita) and its orifice is surrounded by thick sphincteric band.

The/

The right ventricle forms more of the surface of the heart than does the left ventricle; its large size is a common feature of mammalian foetal hearts. Its diaphragmatic surface is slightly convex; its sterno-costal surface is more convex and is continued dorsally and to the left as the infundibulum from which the pulmonary artery arises. The boundary between the infundibulum musculature and the arterial wall is sharp, but two processes of sub-epicardial fat are prolonged on to the sides of the artery; it was determined by dissection that they correspond in position to the intervals between the ventral cusp and the dorsal cusps of the pulmonary valve. The margin between the two surfaces of the ventricle is rounded.

The wall of the greater part of the ventricle is about 10 mm. thick, but the wall of the infundibulum is only about half this thickness. The wall of the left ventricle is 13 mm. thick. The relation of these thicknesses is that commonly found in foetal mammalian hearts; it alters after birth, when the pulmonary circulation is established and the ductus arteriosus is obliterated, and the left ventricle wall becomes two or three times as thick as the right ventricle wall. In the adult Cetacea, however, the right ventricle wall is relatively much thicker, the actual measurements in four specimens being:-

Species	Sex	Length	Thickness		Weight of Heart
			Left V.	Rt. V.	
Sperm	M.	50 ft.	65mm.	40mm.	258 lbs.
Sperm	M.	48 ft.	62mm.	38mm.	245 lbs.
Fin.	Fem.	49 ft.	60mm.	50mm.	270 lbs.
Fin.	Fem.	58 ft.	105mm.	75mm.	320 lbs.

Table 2 . Measurements were made on fresh hearts at the Rose Harbour Whaling Station.

Owen (1868) has associated this increase in relative thickness of the right ventricular wall with the greater driving force that is necessary to force the blood through the lungs.

The cavity of the ventricle has the two typical parts, namely, a posterior receiving part into which the right atrium opens and an anterior expelling part which leads upwards into the infundibulum. The myocardial bundle separating the two parts is well developed, the supraventricular crest being a broad prominence across the roof of the vestibule in front of the A.-V. orifice; the crest is continued ventrally on the septal wall of the ventricle, and, gradually rising/



rising from the surface, leaves it at the ventral part of the cavity as a well developed trabecula septo-marginalis (moderator band) which is 7 mm. in diameter where it leaves the septum. The three cusps of the A.-V. valve are, as usual, ventral, posterior, and septal in position, these being given in the order of their size, the ventral being the largest. A short papillary muscle has an extensive attachment of the moderator band. This muscle gives rise to two rows of chordae tendineae - one lying behind the other - and these are attached to the ventral and posterior cusps respectively.

Attached to the posterior wall there are two distinct muscles which distribute chordae to the posterior and septal cusps. The septal chordae arise directly from the septal wall immediately behind the septal extension of the supraventricular crest, there being no papillary muscle (of Lancisii) at their base. The bases of the cusps of the atrio-ventricular valve are surrounded by a perivalvular space and crossing it to the cusps are chordae tendineae of the third order.

The walls of the apical region of the ventral part of the ventricle are richly and freely trabeculated, but the walls of the upper part and of the infundibulum are, as usual, smooth. The cusps of the pulmonary valve are ventral and right and left dorsal/



dorsal in position.

The left ventricle, conical in form, was studied by means of transverse sections at right angles to its long axis. The average thickness of the wall is 13 mm. The cavity of the ventricle is divided into two parts by the aortic (ventral) cusp of the mitral valve, the postero-lateral part of the cavity receiving the left atrio-ventricular orifice and the antero-medial part leading upwards into the aortic vestibule and the aortic opening. The receiving cavity is everywhere richly trabeculated, but the aortic vestibule is smooth though on its medial wall are two aortic bands which serve to fix the aorta to the ventricular wall; the bands are continued to the apex of the ventricle.

The cusps of the mitral valve are ventral (aortic) and dorsal in position. The two papillary muscles have the same characteristics as those of the right side in that they are but slightly raised masses with a broad attachment to the ventricular wall. The chordae tendinae take linear origin from the muscles, and have the typical distribution to the cusps of the valve.

The cusps of the aortic valve are ventral and right and left dorsal in position, this arrangement being in keeping with the position of the cusps of the pulmonary valve. Murie (1865) in the description of the/

the heart of an adult Physalus antiquorum refers to the absence of nodules on the arterial valve, but I have found them well developed both in my foetal specimens and in the hearts of numerous adult finbacks that I examined.

*W/- This is  
now known as  
Balaenoptera  
musculum*

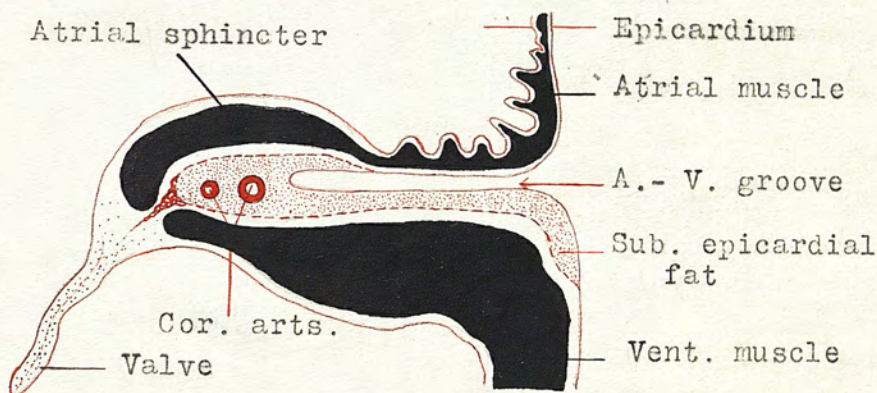


Fig. 13 A diagram of a vertical section through the right atrio-ventricular orifice.

The atrio-ventricular orifices and the atrio-ventricular valves:- A diagram of a vertical section through the right A-V orifice and the ventral cusp of the tricuspid valve is shown in Fig. 13 . The A-V groove is deep and is lined with epicardium which is reflected from the atrium to the ventricle near its deep end. The sub-epicardial fat is accumulated on the/



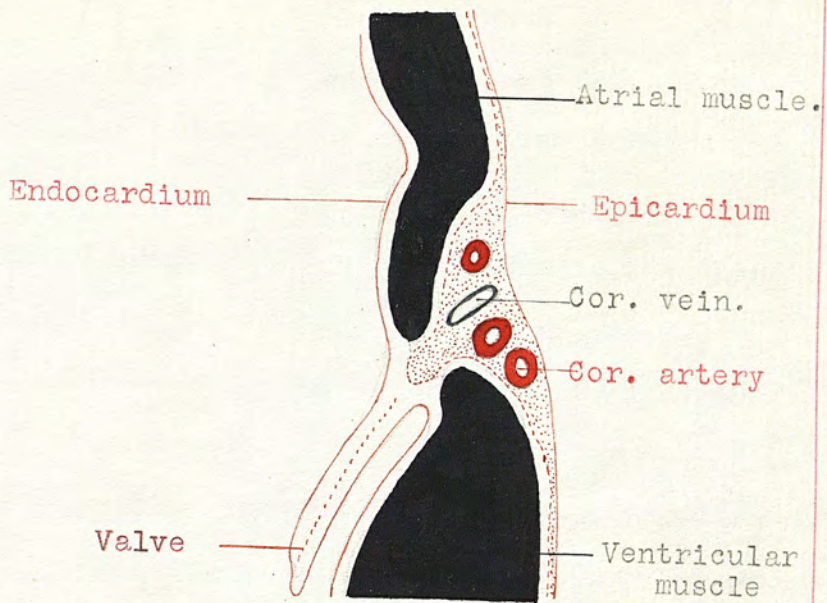


Fig.14 A diagram of a vertical section through the left atrio-ventricular orifice.

the ventricular wall of the groove and is continued beyond the epicardium into the A-V interval; it there contains branches of the coronary artery and separates the atrial and ventricular musculatures. The two musculatures reach the base of the A-V valve. Under x 8 magnification the musculatures are neither continued into the valve nor is there a connexion between them; a process of the sub-epicardial fat appears to be prolonged into the base of the valve. The valve thus seems to be formed of a reduplication of the endocardium and is less fibrous in structure than valves of the human foetus. The atrial sphincter round the A-V orifice is conspicuous.

A vertical section through the left A-V orifice and the dorso-lateral cusp of the ventral valve (Fig. 14 ) shows the A-V groove to be much less deep; but the general arrangement of the parts is the same as at the right orifice. The cusp of the valve, however, is supported on the ventricular muscle rather than hanging free in the ventricular cavity.

At both orifices there appears to be a conspicuous absence of fibrous tissue at the basal attachment of the valve cusps.

The microscopic appearances of the A-V junctions and the cusps of the A-V valves.

The microscopic examination of the A-V junctions confirms the discontinuity of the atrial and ventricular musculatures; they are separated from each other by a fibrous mass that is continuous externally with the sub-epicardial tissue and to which internally the bases of the A-V valves are attached. The cusps are formed of a reduplication of the endocardium with a central fibrous core. There are no extensions of myocardium into them, that is, there is neither ventricular nor atrial muscle in them even at the base, and therefore, even at this stage of development they are non-muscular structures. The central fibrous-tissue part has many cells in it and there are also blood-vessels in its basal third.

The/



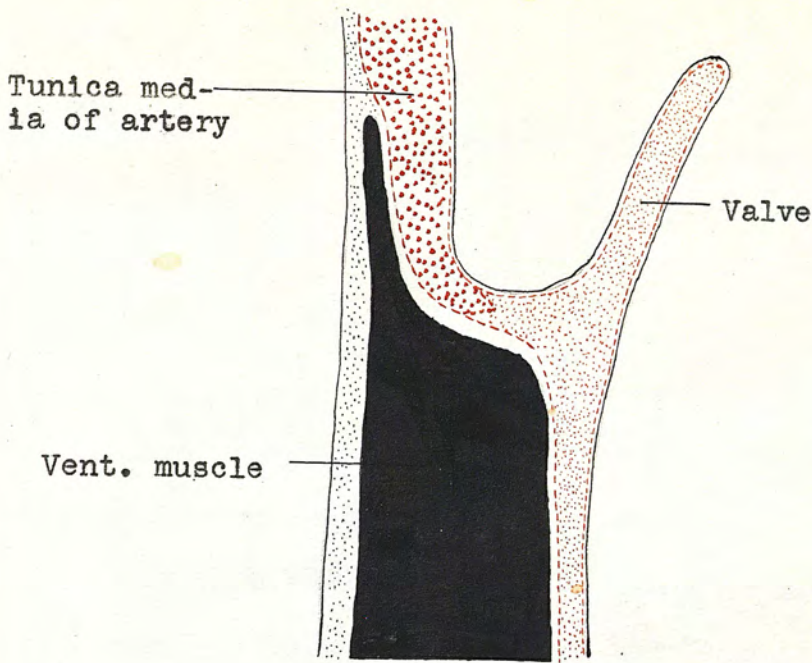


Fig. 15 . Diagram of longitudinal section through the pulmonary orifice to show the relationship of the ventricular muscle to the tunica media of the artery.

The arterial orifices and the arterial valves.-

A longitudinal section through the pulmonary artery and the pulmonary orifice is shown in Fig. 15. The tunica media of the artery is highly elastic and when traced towards the infundibulum it is seen to pass within the cardiac muscle and to lie in the endocardial plane. Conversely, when the muscle of the infundibulum is traced distally it forms a thin lamina which passes without the tunica media and lies in the tunica adventitia of the artery. These observations confirm the accepted morphological interpretation that the cardiac muscle is homologous with the outer coat of the /

the arteries whereas the tunica media and tunica intima together represent the endocardial system of the heart.

A series of transverse sections of the pulmonary artery show a progressive increase in thickness of the arterial wall as it passes from its commencement towards the origin of the ductus arteriosus (which arises directly from the main pulmonary trunk). The right and left pulmonary arteries are relatively as thick-walled as the main trunk until they pierce the pericardium; there the walls suddenly diminish in

Intra-pericardial part of artery

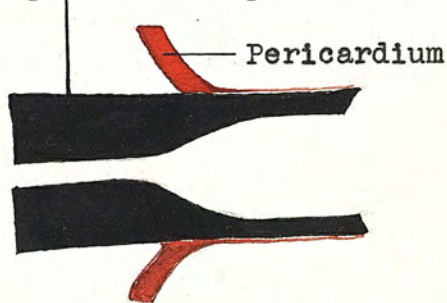


Fig. 16 . Diagram to show diminution in thickness of the wall of a pulmonary artery as it pierces the pericardium.

thickness.

The structure of the aortic orifice is essentially similar to that of the pulmonary orifice and the intra-pericardial part of the aorta is in like manner thick-walled (see ascending aorta and arch of aorta).

The ductus arteriosus passes from the termination of the main pulmonary stem to the aortic arch at the level./



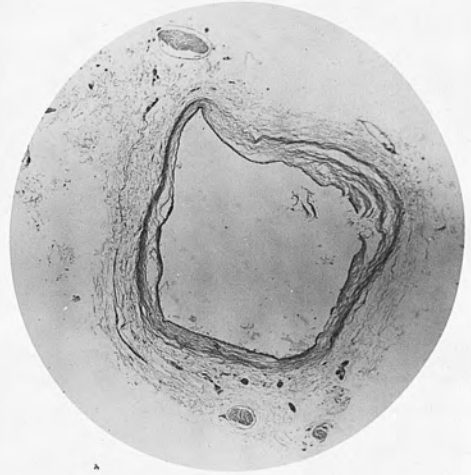
level of the interval between the origin of the left carotid and subclavian arteries. The duct is 10 mm. long, has an external diameter of 8 mm. at its midpoint, where its wall is 3 mm. thick; at its pulmonary attachment it has a larger calibre.

The ductus arteriosus is characterised by the thickness of its wall. By far the greater part of the wall is composed of fibrous tissue in which there are a few muscle fibres, and this part of the wall I consider to be the tunica adventitia; the tunica media, as is sometimes also the case in the larger veins, is absent. The internal elastic lamina is in two layers; the inner layer is scalloped but the outer is regular and even. The endothelium has been denuded so that the tunica intima is represented by the internal elastic lamina along with a few smooth muscle cells that separate the two elastic layers. It may be that the outer elastic layer represents the normal external elastic lamina and that the tissue between the two layers is homologous with the normal tunica media.

The ductus arteriosus in specimens Nos. 3 and 4 has a similar structure and this form of ductus stands in contrast to that which is normally met with in land mammals. The typical ductus arteriosus, as is met with in the human foetus, has a thin venous-like wall which /



(a)



(b)

Fig. 17 . Photomicrographs of transverse sections of ductus arteriosus of (a)Foetus No. 3, and (b)Human foetus 22 weeks old.

which is composed of a single elastic lamina lined internally by endothelium and bounded externally by fibrous tissue in which there may or may not be a few muscular and elastic fibres. The structure of the ductus arteriosus is thus normally more like the structure of a typical vein, and its great thickness in the whale is not singular in view of the structure of some of the intestinal and subcutaneous veins. In some of the intestinal veins in both the adult and foetal finback the wall is thicker than the wall of the corresponding artery, but in contrast to the artery the wall is mainly composed of fibrous tissue, in the adventitia of which there is a variable amount of elastic tissue. All gradations between this thick walled vein and the vein of normal thickness can be seen in the veins of different viscera.

This interpretation of the structure of the ductus arteriosus has not been advanced before, but in view of the conflicting opinions of the manner of the post-partum closure of the ductus it assumes considerable importance. The one view that the closure of the ductus is effected by the contraction of the muscle fibres of its wall is not substantiated by the evidence that I have adduced, but it does support the view that the closure is mechanically effected by a process of torsion which acts on the ductus through the /

the pull of the pericardium in the inspiratory descent of the diaphragm. When the ductus is comparatively thin-walled it is easy to understand its functional occlusion quickly taking place; but when it is so thick-walled as in the Cetacea it is possible to conceive that it may remain patent for some time and, indeed, until organic occlusion occurs by the structural changes in its wall. a

The pulmonary stem, the ductus arteriosus, and the intra-pericardial parts of the aorta and the right and left pulmonary arteries are thus characterised by their thick walls, a condition that is not maintained in their extra-pericardial parts.



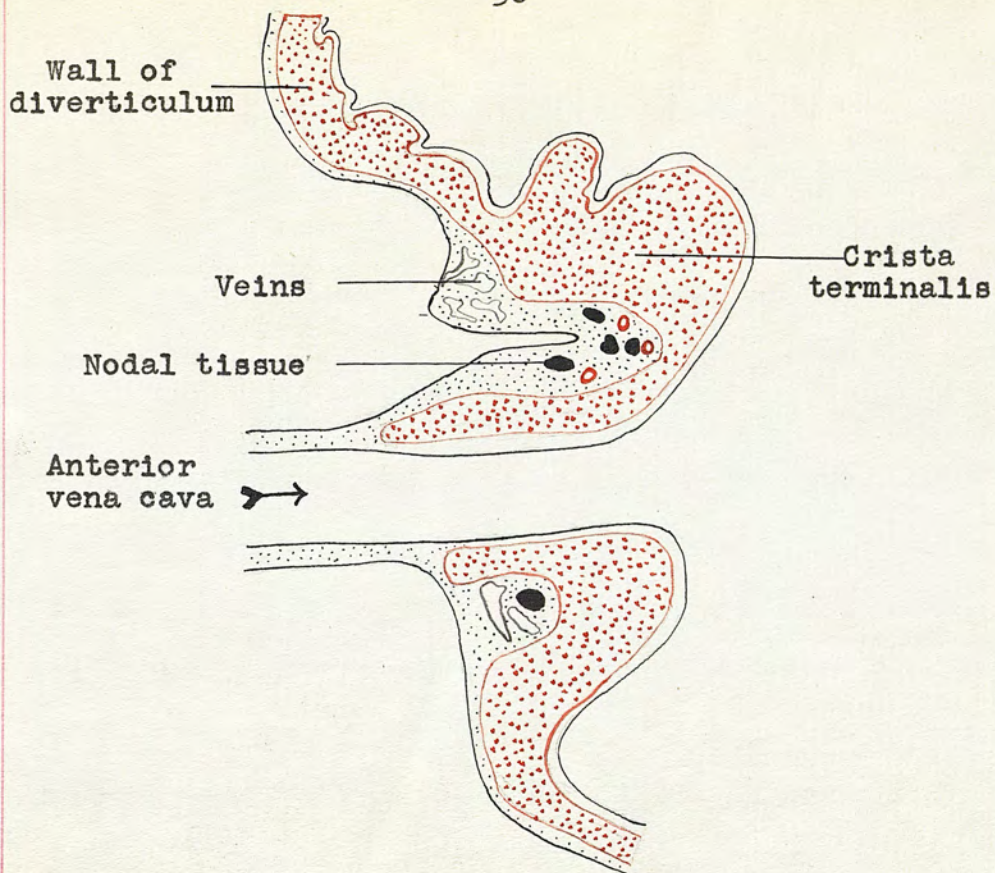


Fig. 18 . Diagram to illustrate the position of the sino-atrial node.

### The Conducting System of the Heart

The condition of the hearts of the foetuses did not allow a detailed examination of this system to be made but the following facts were established:

The sino-atrial node was sought and discovered in a block which was removed from the right atrium and included the root of the anterior vena cava and the dorsal part of the sulcus terminalis. The node is in the form of several undifferentiated masses/which lie/



lie deeply in the sub-epicardial tissue in the anterior part of the sulcus terminalis; there is also a single group of cells which lies dorsal to the root of the anterior cava. Numerous veins and arteries are associated with the node.

The node is easily distinguished from the cardiac muscle. The masses consist of large oval nuclei, closely aggregated and staining densely, which are surrounded by a small amount of faintly stained protoplasm in which there is neither a longitudinal arrangement nor striation; it contains, however, large numbers of small dark granules which are not present in other parts of the section.

The atrio-ventricular (A-V) node was sought and discovered in a block removed from the ventral part of the septal wall of the right atrium. The

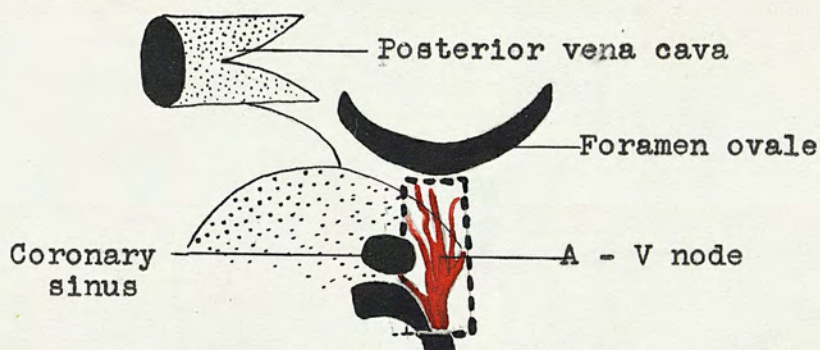


Fig. 19 . Diagram to show part of right atrium removed for microscopic section.

area of the block is shown in figure 19; it included the ventral margin of the foramen ovale, the anterior part of the coronary sinus and the margin of the atrio-ventricular orifice. It was also thick enough to/



to include a part of the septal cusp of the tricuspid valve, the dorsal end of the ventricular muscle and the fibrous tissue between the right atrium and ventricle.

The block was cut vertically from left to right in serial sections  $10\mu$  thick.

The A-V node is a small oval body which lies deep to the endocardium in the fibrous tissue of the atrial wall close to the atrio-ventricular junction and immediately above the base of the septal cusp of tricuspid valve (Fig.20); overlying it there is a

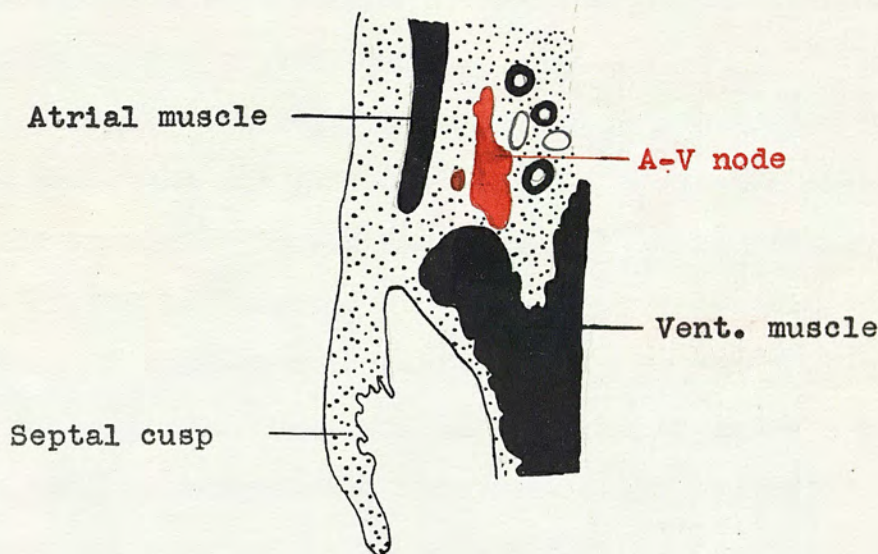


Fig. 20 . Diagram to illustrate the position of the atrio-ventricular node

thin strip of vertical atrial muscle. At its left end the node is continued into the A-V bundle which in the end section of the series is still in the fibrous tissue above the ventricular muscle. At its right end the node is seen to be formed by a number of branches which come from all directions. The formation and position/

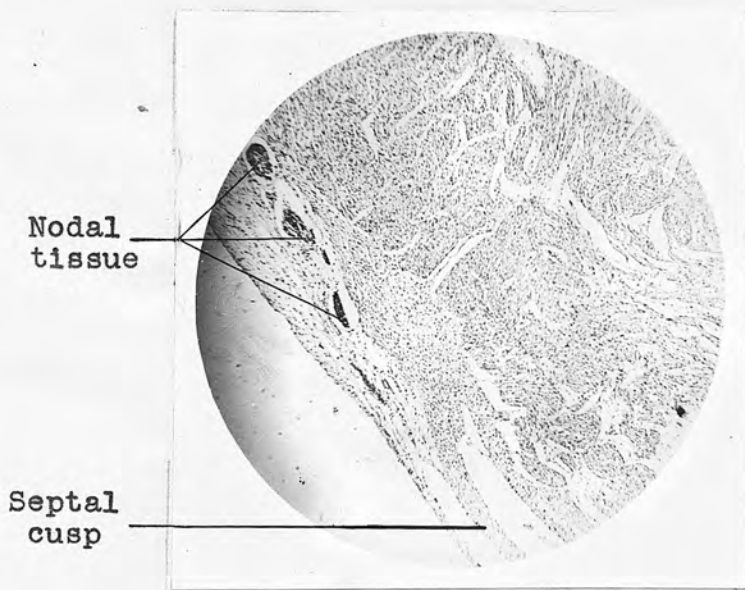
position of the node are shown diagrammatically in figure 19.

The histological structure of the A-V node is similar to that of the sino-atrial node; photomicrographs of the nodal tissue are shown in figure 21.

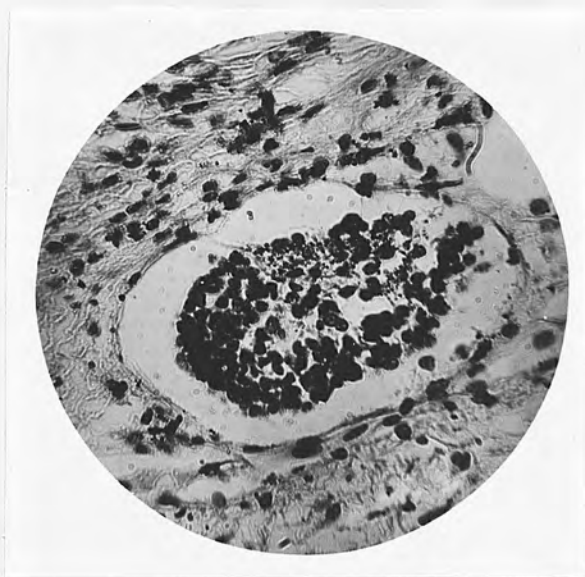
In seeking for the atrio-ventricular bundle I made and examined a series of transverse sections of the interventricular septum and the moderator band. I was unable, however, to find any evidence of either the right or the left limb of the bundle, but this was not surprising in view of the poor histological condition of these parts of the heart.

I attempted on several occasions to expose and inject the right and left limbs of the atrio-ventricular bundle in adult finback and sperm whales but was always unable to detect naked-eye any part of this system. I removed a number of pieces of the septum and the moderator band and in sections of these I have been able to demonstrate microscopically Purkinje fibres and parts of the bundle (Fig. 22).

White and Kerr (1915) have described some parts of the conducting system in the sperm whale and liken the condition there found to that in ungulates.

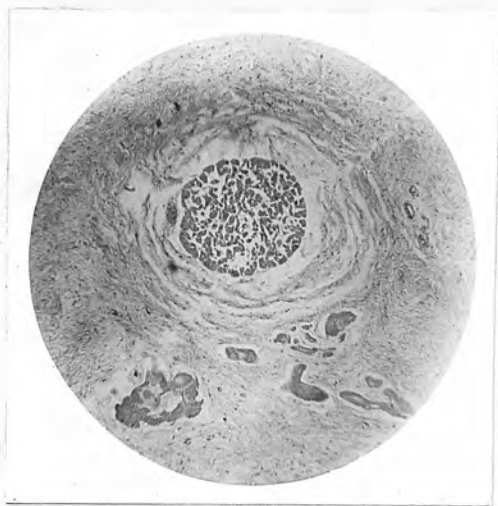


(a)



(b)

Fig. 21. Photomicrographs of A-V node: (a) is low power magnification and shows the septal cusp, and (b) is high power and shows the delicate sheath round the closely aggregated cells which form the node.



(a)



(b)

Fig. 22 . A transverse section of the right limb of the A-V bundle in the moderator band is shown in (a); Purkinje fibres, also from the moderator band, are shown in (b).



CORONARY VESSELS.

The arterial supply of the heart is by two coronary arteries - a right and a left. They arise from the aortic sinuses, which are so situated that they must be termed a right and a left ventral and a dorsal, and they are distributed in a manner which falls within the common mammalian pattern.

The right coronary artery arises from the right ventral aortic sinus and passes to the right, first between the aorta and the pulmonary artery and then under cover of the right auricle as far as the right border of the heart. Lying in the coronary sulcus it turns round onto the dorsal surface of the heart where it immediately divides into two equally sized branches that continue to the left as far as the posterior interventricular groove. Before reaching the groove the posterior of the two branches gives off an additional branch that has a course parallel and immediately adjacent to the main trunks. The three branches inosculate with each other and pass in the posterior interventricular groove almost as far as the interventricular notch; they give branches to both ventricles. The right coronary artery also gives off the following branches. - (a) An infundibular branch, almost/



branch, almost as big as the parent trunk, arises from its commencement. This branch turns onto the ventral surface of the infundibulum on which it breaks up into a series of branches. (b) Several small branches to the right atrium and auricle. (c) A right marginal branch that gives twigs to the ventral and diaphragmatic surfaces and reaches to within a short distance of the interventricular notch.

The left coronary artery arises from the left ventral aortic sinus and passes to the left with the usual relationship to the left auricle and the pulmonary trunk. It turns round the left border of the heart and continues for a further 25 mm. where it terminates by dividing into four small vessels that are distributed to the left ventricle; none of these terminal vessels reach quite as far as the interventricular groove. The left coronary artery gives the following branches.- (a) The ventral interventricular artery which is larger than the continuation of the parent trunk. It passes distally in the interventricular groove as right and left branches that are distributed to the respective ventricle and terminate on the diaphragmatic surface of the heart. A short distance from its origin the interventricular artery gives off a stout branch that ramifies on the ventral surface of the infundibulum. (b) A left marginal artery that passes to within a short distance of/

the  
of/interventricular notch.

Beauregard and Boulart (1897) have drawn attention to the completion of the arterial circle on the ventral surface of the infundibulum in two young Balaenoptera (musculus at rostrata) by means of leashes of small vessels from the two pulmonary arteries. This is in contrast to the condition in Man where the arterial circle is completed by single right and left branches. Pouchet and Beauregard (1889-1892) in addition to noting the infundibular anastomoses in Megaptera nodosa also found anastomoses between the marginal arteries and the ventral interventricular arteries. I was unable to establish these anastomoses in any of my specimens although I found that in the situation of them the respective arteries came into close relationship with one another.

Coronary vessels of a 58 feet long female finback.

The heart of this specimen weight 320 pounds. The distribution of the arteries was essentially similar to that which has been described for the foetus, and they showed the same tendency to form collateral trunks.

The left coronary artery had an external diameter of 4 cm. and gave off a ventral interventricular branch 7 cm. from its origin; this vessel had a diameter of 3 cm. and the continuation of the parent stem/

stem was 3 cm. The left marginal artery had a diameter of 1.5 cm.

The right coronary artery had a diameter of 3 cm; its atrial branch was 1 cm. wide and its marginal branch 1.5 cm. In the dorsal part of the atrio-ventricular sulcus the main stem divided into three equally sized branches that passed distally in the interventricular groove.

The coronary veins (in foetus No.1) have the usual mammalian distribution although they are typical of the Cetacean venous system in that the single mammalian vein is represented by multiple channels. The oblique vein (of Marshall) is large and pervious and forms a well defined vestigial fold.

THE SYSTEMIC ARTERIES

The aorta is typically mammalian in character in that it possesses an ascending part, a transverse part that arches over the root of the left lung and a descending part that lies in the thoracic and abdominal cavities. Although the terms "ascending" and "descending" are not correct when used in relation to the supine position these terms are retained on account of their universal use in comparative anatomy. Despite the variation in the position of the heart and the variability of the inclination of its long axis in the various Cetacea, the aortic arch is usually strongly curved, as in this specimen.

The ascending aorta is 25 mm. long and passes forward and to the right behind the second right costal cartilage. It is overlapped ventrally by the pulmonary artery and the right auricle and terminates in the arch of the aorta at the anterior border of the cartilage and about 20 mm. to the right of the median plane.

The arch of the aorta commences at the upper border of the second right costal cartilage and passes dorsally and to the left with a typical double curvature to terminate in the descending aorta at the level of the fifth thoracic vertebrae. Dorsal and to the right/

right of the aortic arch there are in succession the laryngeal sac\*, the trachea, the oesophagus (which lies quite to the left of the sac at this level) and the vertebral column. Ventrally the pericardium extends forward on to the arch and this separates it from the discrete right and left thymus glands. Between the left gland and the arch there are the vagus, cardiac, and phrenic nerves, the last of which lies in a fold of pleura as is shown in figure 8. Posteriorly there are the bifurcation of the pulmonary artery, the root of the left lung, the ductus arteriosus; the recurrent laryngeal branch of the left vagus nerve hooks round the aorta dorsal to the ductus arteriosus.

The/

\* The laryngeal sac is proportionately larger in this specimen than any that I have so far seen recorded or otherwise examined. It has a maximum length of 70 mm., its greatest breadth is 45 mm. and its apex extends just beyond the bifurcation of the trachea. The outer muscular coat is comparatively thin and is attached ventrally to the posterior margin of the thyroid cartilage and dorsally to the cricoid and laryngeal cartilages; the muscular fibres are arranged in the manner illustrated in figure 1. The cavity of the sac is almost obliterated by the apposition of its walls and it communicates with the larynx through a deficiency in the ventral wall of the cricoid cartilage. The wall of the sac is 15 mm. thick and is largely composed of sinusoidal tissue, the walls of which are made up of smooth muscle in which there are a few elastic fibres. The sinusoidal spaces are lined by endothelium and in some of them there are blood corpuscles. The structure of this tissue is seen in Fig. 23. The sac is supplied on each side by two small branches that arise from the carotid arteries and also by twigs from the thyroid arteries. Several veins pass from it to drain into the innominate trunks.

23



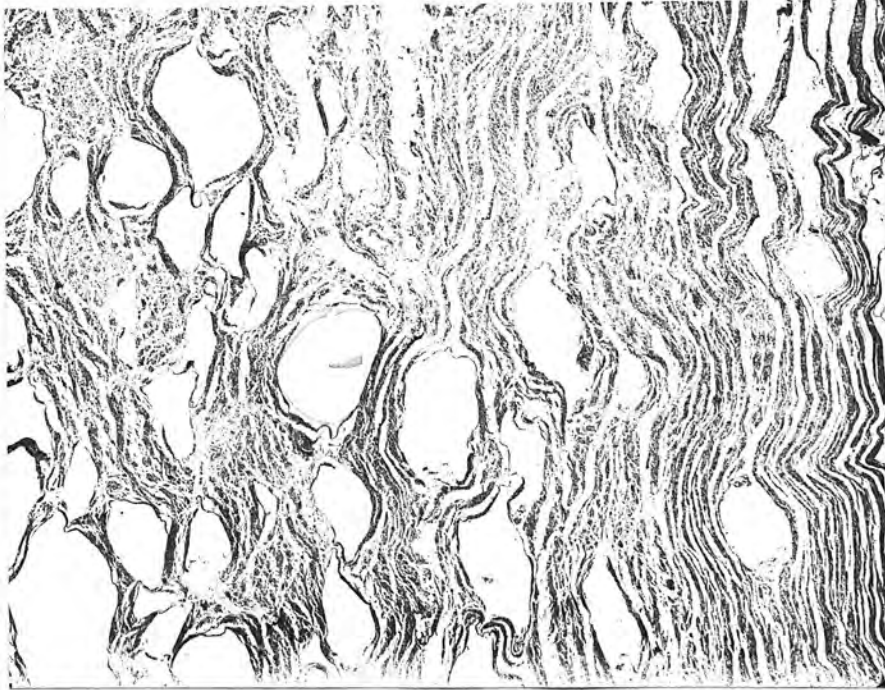


Fig. 23 . Section of laryngeal sac (X 20).  
The outer muscular coat is to the right of  
the figure.

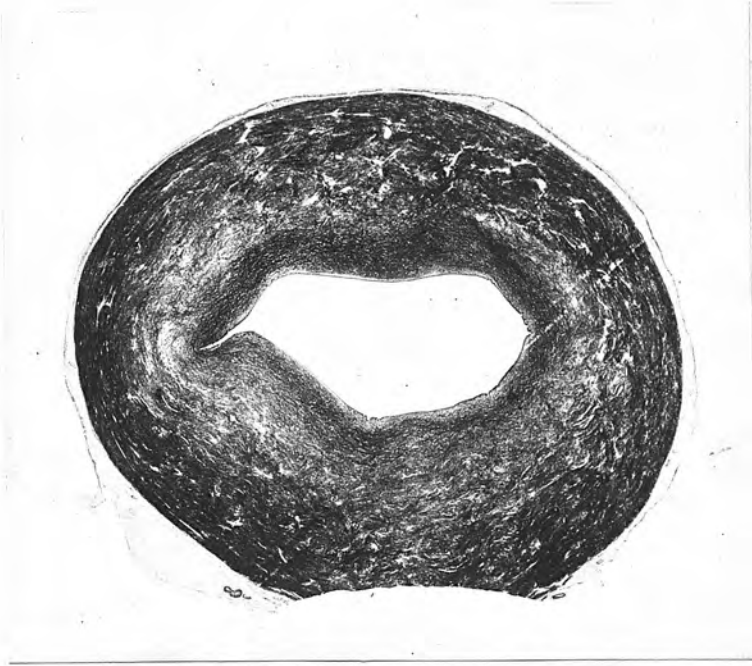
The intra-thoracic position of the aortic arch is found generally in the Balaenopteridae and is in contrast to the condition in the Odontoceti, which has been described by Slijper (1936), where the arch lies at about the level of the thoracic inlet.

The nature of the ascending aorta and the intra-pericardial part of the aortic arch, which is proximal to the entrance of the ductus arteriosus, is unusual. Although the external circumference of this part of the vessel namely 60 mm., is remarkably constant, the size of the lumen varies owing to a change in the thickness of the arterial wall. Immediately beyond the aortic sinuses the wall is 5 mm. thick, at the junction of the ascending aorta and the arch it is 9 mm. (cf. pulmonary artery) and at the level of the entrance of the ductus arteriosus it has decreased to 6 mm. The entrance of ductus arteriosus into the aorta and the attachment of the fibrous pericardium correspond in position and are opposite the interval between the origin of the left common carotid and the left subclavian artery. The rapid thinning of the wall distal to the entrance of the ductus is very striking for in 10 mm. from its entrance it decreases from 6 mm. to 2 mm. The thickened condition of the ascending aorta and the proximal part of the arch was noted by Schulte (1916) in his dissection of a 375 mm. foetal/

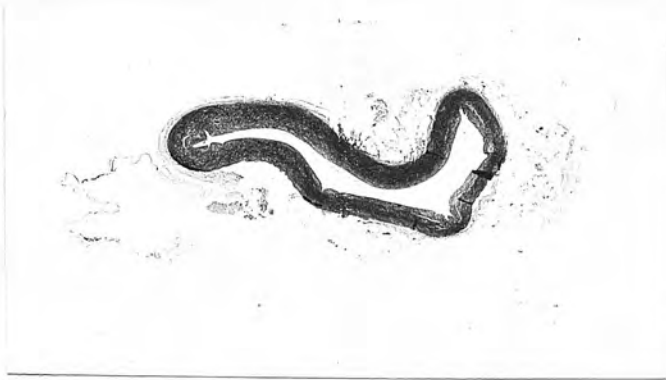
foetal *Balaenoptera borealis*. In his description he states that in that part of the aorta the lumen is reduced to a mere slit between two longitudinal cushion-like ridges above the sinuses of Valsalva and that the vessel does not attain a circular lumen until it receives the ductus arteriosus. I am unable to confirm the presence of the longitudinal cushions described by Schulte: the wall is of a fairly uniform thickness in all transverse sections. The appearance of a transverse section of the ascending aorta is shown in fig. 24a ; the indentation present in it is an artefact and was not apparent either proximal or distal to the block from which the section was made.

The tunica media forms the greatest part of the wall and is composed of the typical fenestrated elastic membranes that are characteristic of the larger vessels. It is unusual, however, for a vessel with such a structure to be so thick walled; the ascending aorta of a 22 week human foetus shows the usual mammalian condition. The great difference in the thickness of aorta distal to the entrance of the ductus arteriosus is shown in figure 24b , which is at the same magnification as figure 24a.

The branches of the arch of the aorta are also thick walled, at least at their commencement, and there is a definite relationship between the thickness of/  
of/



(a)



(b)

Fig. 24. Transverse section of (a) ascending aorta, and (b) descending aorta at the level of the fifth thoracic vertebra. Both sections are at the same magnification (X5).





Fig. 25 . Transverse section of ascending aorta of 22 week human fetus (X25). This vessel is typical of the ascending aorta of land mammal fetuses and is in contrast to that shown for the finback whale fetus in figure 24a.

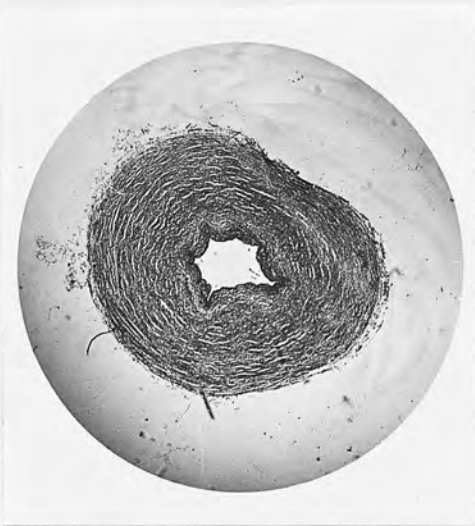
of the arch and the thickness of the branches. Thus the wall of the innominate artery is thicker than the wall of the left subclavian, this being in keeping with the decreasing thickness of the arch. The structure of the branches is typical in that the media has the usual elastic-muscular composition. This is in contrast to the structure of the wall of the ductus arteriosus, the wall of which is composed for the most part of fibrous tissue.

The Branches of the Arch of the Aorta. Three vessels arise from the aortic arch, namely, the innominate, the left common carotid, and the left subclavian artery. In most Cetacea the branches of the aortic arch are two innominates, but in the Mysticeti the aortic arch pattern is usually as in this specimen; in the other three fetuses there was a similar pattern. Ommanney (1932a) found the same arrangement in two foetal finbacks.

Owen (1868) drew an analogy between the mode of origin of the branches of the aortic arch and the breadth of the chest. As extreme examples he quoted the narrow-chested ungulates where there is a single innominate trunk and the broad flat-chested Sirenia, where the branches arise as they do in the finback, and there is also a partial severance of the ventricles. Slijper (1936) associates the mode of branching more with/



(a)



(b)



(c)

Fig. 26 . The three photomicrographs are transverse sections of innominate(a), left common carotid(b) and left subclavian(c) arteries. Each transverse section is taken from the vessel very near its commencement and shows the relative difference in thickness of the walls.

with the dimensions of the thoracic inlet rather than with the breadth of the chest as a whole.

In my specimen the innominate artery arose from the arch 20 mm. to the right of the median plane, the left carotid 50 mm. distal to it, and the left subclavian 10 mm. from it. The main difference between the origin of these branches and the corresponding branches in Man - one of the few forms where there is a similar type of branching - is the greater distance between the innominate and the left carotid, and this can well be accounted for by the relative difference in the size of the thoracic apertures.

The innominate artery arises from the aortic arch at the level of the second costal cartilage and about 20 mm. to the right of the median plane; it has an external diameter of 10 mm. It passes forwards, dorsally, and to the right for 30 mm. and terminates by dividing into the right subclavian and right common carotid arteries. On the lateral side of the innominate artery is a deep process of the thymus gland which separates the artery from the anterior cava and the right innominate vein, and on the medial side there are the laryngeal sac and, more anteriorly, the lateral lobe of the thyroid gland in which the artery is embedded. Ventrally the artery is directly related to the left innominate vein which separates it from/



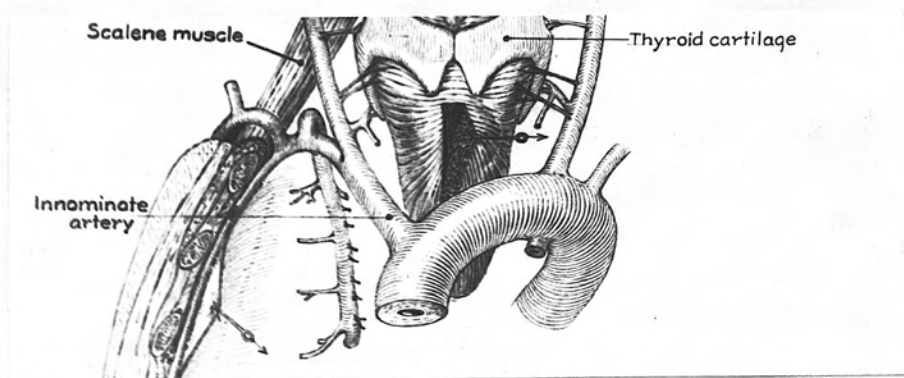


Fig. 27 . Branches of the arch of the aorta.

from the right thymus gland, and dorsally it is in contact with the right vagus nerve. The innominate artery gives off no branches except its terminals.

The right subclavian artery arises from the innominate artery at the level of the 1st costal cartilage; at its origin it has an external diameter of 6 mm. It passes almost directly laterally as far as the origin of its internal thoracic branch and then curves sharply forwards and arches over the 1st rib at the outer border of which it is continued into the axillary artery. The subclavian artery lies dorsal and a little posterior to the right subclavian vein, and between the two vessels there are the vagus, cardiac, and phrenic nerves, in that order from the medial to the lateral side; the recurrent nerve hooks round the subclavian artery. The right innominate vein is also ventral to the medial part of the artery and its costo-cervical tributary hooks around the artery from the dorsal to the ventral side. Superficial to the veins there are the infra-hyoid, sterno-mastoid, and sterno-mandibularis muscles. The most important dorsal relation of the artery is the scalenus medius muscle with which the artery is in direct contact; the scalenus anterior muscle is absent.

Branches./

Branches.

(a) The inferior thyroid artery is an exceedingly small branch that arises from the anterior surface of the subclavian close to its commencement and almost immediately sinks into the closely adjacent posterior pole of the lobe of the thyroid gland. I am not aware of any previous description of this branch of the subclavian but I was able to confirm its presence on four occasions.

(b) The costo-cervical trunk is the second, and largest branch of the subclavian, and is the one that has probably attracted more attention than any other individual artery in the Cetacea. The artery owes its importance to its close association with the thoracic and cervical retia mirabilia, the largest of all the retia in Cetacea.

In the British and American literature this artery has usually been termed the posterior thoracic, a name first introduced by Stannius (1841). As the artery is limited in its course to the anterior part of the dorsal thoracic wall, the term is descriptively poor, and as its distribution is essentially similar to, although more extensive than, the costo-cervical trunk of other mammals I have no hesitation in adopting that term in this work. In addition to being termed the posterior thoracic artery, this trunk has/

has also been referred to as the Art. Mir. Thorac. Cerv. by Barkow (1866) and the thoracique interne by Bouvier (1889).

The costo-cervical trunk arises from the subclavian 10 mm. from its commencement and at its origin has a diameter of 5 mm. It arches dorsally with a well defined curve as far as the neck of the first rib where it divides into its two terminal branches that I propose to call the dorsal thoracic and the deep cervical. Although the lungs in the specimen were collapsed it is obvious that the apex of the lung with its covering pleura and fascia would be closely related to this part of the vessel.

(1) The dorsal thoracic branch (superior intercostal) runs backwards and medially as far as the fourth intercostal space to terminate as the fourth dorsal intercostal. It lies ventral to the necks of the ribs and dorsal to the parietal pleura, and in this part of its course it is immediately lateral to the sympathetic trunk and medial to the companion vein which commences at the sixth intercostal space. The artery is also in close relationship medially with the lateral edge of the thoracic rete mirabile, which in a foetus of this size is but poorly developed. Arising from the dorsal thoracic artery are the dorsal intercostal branches for the first four spaces. These have the usual muscular and nerve relationships in the spaces/



spaces and do not (as verified by microscopic section) terminate in a leash of branches, as they are usually stated to do; they anastomose with the intercostal branches of the internal thoracic artery. From the roots of the intercostal arteries there take origin the dorsal thoracic branches which pass through the substance of the thoracic rete mirabile into the epaxial muscles in which they terminate; they give off small spinal branches. From the dorsal thoracic artery and the dorsal branches of the intercostal there arise innumerable small vessels which enter the substance of the thoracic rete mirabile and, indeed, form its arterial component; these will be described along with the retia mirabilia.

(2) The deep cervical artery, the other terminal branch of the costo-cervical trunk, passes dorsally through the process of the rete mirabile that lies between the neck of the first rib and the seventh cervical transverse process. In that situation the artery divides into an anterior and a posterior branch. The posterior branch passes directly dorsally to ramify in the muscles of the adjacent region and the anterior branch passes forward to supply the epaxial muscles that overlies the cervical vertebrae.

(c) The internal thoracic (mammary) artery arises from the subclavian artery at the medial border/

border of the scalenus medius muscle; at its origin it has a diameter of 3 mm. It passes backwards on the inner surface of the chest wall, mid-way between the ventral and dorsal surfaces, as far as the fifth intercostal space where it terminates by dividing into a small anterior epigastric and a much larger musculo-phrenic branch. The artery is accompanied by venae comites that enter the subclavian vein and there are numerous lymph glands lying superficial to it. It gives off the following branches.- (1) A pericardial branch arises directly from the root of the internal thoracic and passes superficial to the thymus glands, to which it gives branches, and terminates on the ventral surface of the pericardium. (2) The pericardiaco-phrenic arises 15 mm. from the commencement of the trunk and passes dorsally to join the phrenic nerve which it accompanies to the diaphragm. In its course it gives branches to the thymus, the pericardium, and the pleura. (3) Ventral and dorsal branches ramify on the inner surface of the internal intercostal muscles, and effect anastomoses with the dorsal thoracic artery and the aorta. (4) The musculo-phrenic artery divides opposite the eighth costal cartilage into ventral and dorsal branches, which, along with the main trunk, supply the intercostal spaces and the diaphragm. (5) The anterior epigastric/

epigastric artery passes backwards between the slips of origin of the diaphragm and breaks up into fine twigs that pervade the substance of the rectus muscle; no anastomosis with the posterior epigastric could be determined.

(d) The suprascapular artery arises from the subclavian as it becomes the axillary artery; at its origin it has a diameter of 2 mm. It passes forward and dorsally deep to the sterno-mastoid muscle and in this part of its course gives off numerous vessels which pass into the substance of the sterno-mandibularis. The main trunk continues deep to the omohyoid and breaks into a leash of branches which pass into the supraspinatus muscle; in addition to supplying that muscle branches are also given to the infraspinatus, the teres minor, and deltoid muscles.

In *Phocaena phocaena* the suprascapular artery arises from the omo-occipital trunk; this last named artery is not present in the Mysticeti as the occipital artery <sup>arises</sup> from the external carotid and thus conforms to the ungulate rather than the carnivore arrangement.

The venous trunk which accompanies the suprascapular artery opens into the subclavian vein. In addition to receiving the venae comites of the branches of the artery, it also received a large vein that passes backwards on the scalenus posterior - and drains /

drains the occipital muscles.

The axillary artery extends from the outer border of the first rib to the level of the head of the humerus where it terminates by dividing into the brachial and ulnar arteries. The axillary artery is ventral to the subscapularis muscle but is separated from it by the musculocutaneous nerve, the posterior cord, and the ulnar nerve; it is dorsal to the pectoralis muscle.

Branches:- (a) A small branch to the scalenus posterior. (b) Three lateral thoracic branches which pass caudally on the superficial surfaces of the scalenus posterior and external oblique muscles. Each of those vessels almost immediately after it takes origin breaks into a leash of branches which supply the adjacent muscles. (c) At the same level as the last named vessels there arise two branches which turn round the cranial border of the pectoralis muscle to gain its superficial surface where each breaks up into a series of branches which supply the overlying panniculus carnosus; their terminal twigs extend as far as the umbilicus. (d) A small ventral circumflex branch which passes around the proximal part of the humerus closely applied to the bone. (e) Near its termination the axillary artery gives off a trunk from which there arise the dorsal circumflex and subscapular/



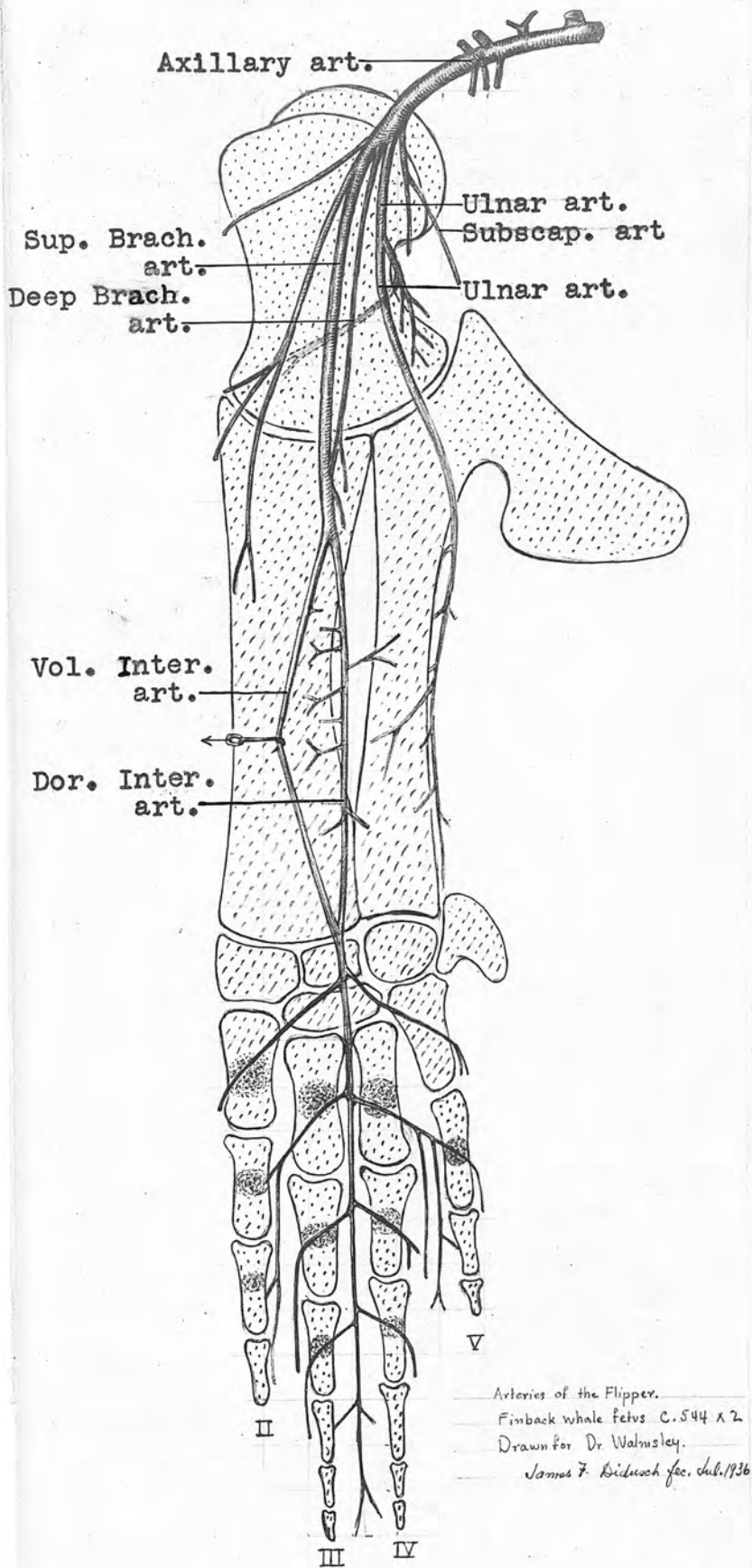


Fig. 28 . Arteries of the flipper.

subscapular arteries; the trunk is 7 mm. long and 3 mm. wide. (1) The dorsal circumflex is smaller than the ventral circumflex artery and passes dorsally between the triceps and the humerus to end in periosteal and deltoid branches. (2) The subscapular branch, which is really the continuation of the trunk, gives off the small circumflex scapular and continues along the lateral border of the scapula supplying minute twigs to the adjacent muscles. Carte and Macallister (1871) in their description of a 16 feet long *Balaenoptera rostrata* state that the axillary artery terminates by dividing into a brachial and "an artery that ran along the inferior border of the scapula". The later branch is akin to the subscapular stem I have described.

Any terminology that is adopted in regard to the terminal branches of the axillary artery will undoubtedly be open to question but it is here taken that the axillary artery ends by dividing into ulnar and common brachial branches.

The ulnar artery passes distally lying on the teres major, the bicipital ligament (the regressed biceps brachialis) and the triceps to the interval between the flexor carpi ulnaris and flexor digitorum. In the forearm it lies close to the medial side of the ulna with the ulnar nerve immediately behind it, and it/

it terminates at the distal end of the ulna by dividing into several branches which go to the post-axial carpal bones and the subcutaneous tissues. About mid-way down the humerus it gives off a relatively large trunk which passes dorsally with the radial nerve and terminates in the triceps muscle.

The common brachial artery is extremely short for it divides almost immediately into a superficial brachial and a deep brachial artery.

The deep brachial artery is an extremely narrow branch which passes distally deep to the superficial brachial artery and is separated from it by the musculo-cutaneous nerve and the bicipital ligament; it joins the superficial brachial a little distant to the elbow joint, after having given off several muscular and periosteal branches.

The superficial brachial artery is much the larger of the two terminal vessels. It traverses the distal part of the axilla ventral to the subscapularis and teres major muscles, and then passes into the arm superficial to the bicipital ligament and the ventral surface of the humerus to terminate 10 mm. distal to the elbow joint by dividing into ventral and dorsal interosseous branches. During its course in the arm the/

the artery passes superficial to the nerve which supplies the flexor digitorum and flexor carpi radialis muscles and the skin of the pre-axial margin of the flipper. This nerve is termed by Schulte (1916) the "musculo-cutaneous" nerve and it crosses the artery from the medial to the lateral side, whereas the medial cutaneous nerve of the forearm crosses superficial to the artery from the lateral to the medial side.

The superficial brachial artery gives off near its proximal end a small radial branch that traverses the upper arm and the forearm in company with the lateral cutaneous branch of the musculo-cutaneous nerve; it supplies the periosteum of the humerus and the radius and the subcutaneous tissue of the pre-axial part of the forelimb. The dorsal interosseous branch passes directly into the interosseous membrane which is a relatively thick structure with a wide attachment to both forearm bones. The artery descends in the substance of the membrane and gives off numerous branches to the bones; it also sends twigs through the dorsal part of the membrane to the extensor digitorum and the subcutaneous tissues. In the distal part of the forearm the artery once again passes into the volar compartment of the forearm to unite with the volar interosseous artery. The volar/



volar interosseous branch passes distally in the forearm between the flexor digitorum and the flexor carpi ulnaris; the artery is deeply placed between these structures and is crossed superficially by the musculocutaneous nerve. It supplies the two muscles and the superficial tissues of the volar aspect of the forearm and is joined at the wrist by the dorsal interosseous artery. From there onwards the artery passes distally as a medial digital trunk in the interval between the third and the fourth digits and crosses superficial to the flexor tendons of the fourth and fifth digits. A series of branches arise from both its radial and ulnar sides and these, as they pass to the borders of the flipper, are intimately related to the ossific centres of the phalanges which they supply.



Fig. 29 . Transverse section of the forearm. The dorsal interosseous artery lies in the interosseous membrane.

VEINS OF THE FLIPPER.

The flipper, like the rest of the foetus, is characterised by the great wealth of venous channels, both small and relatively large, which pervade its tissues. This wealth of veins has frequently been alluded to and is a feature common to all Cetacea.

For the purpose of description the veins of the flipper may be divided into three groups, but it has to be understood that not only is there a free anastomoses between veins of the same group but also between veins of different groups.

(1) Several relatively large veins lie close to the main arteries and unite proximally to form two axillary veins. The axillary veins receive, either directly or indirectly, most of the other veins of the flipper, but even so they are relatively narrow, as there are several anastomotic channels which pass between their distal parts and the intercostal, lateral thoracic, and subscapular veins. It is by these anastomotic channels that the greater part of the venous drainage of the flipper is effected. Proximally the two axillary veins join the dense plexus of veins which passes backwards on the scalenus muscle and by their union they form the subclavian vein.

(2) Small veins are embedded in the tunica adventitia/

adventitia of the brachial, ulnar and interosseal arteries (Fig. 30). There may be from two to six such veins in relation to one artery, and as there are frequent anastomoses among them the number varies at different parts of the same artery.

(3) Numerous veins pervade the muscles and the subcutaneous tissues (Fig. 31).

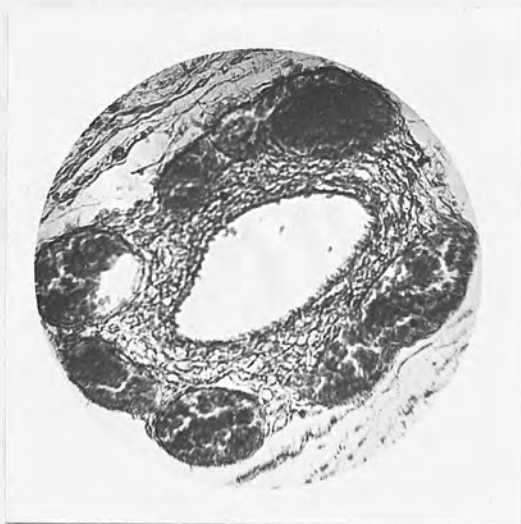


Fig. 30 . Artery with veins embedded in adventitial coat.



Fig. 31 . Skin and superficial tissues of flipper. (X 200). The irregular dark areas are congested veins.

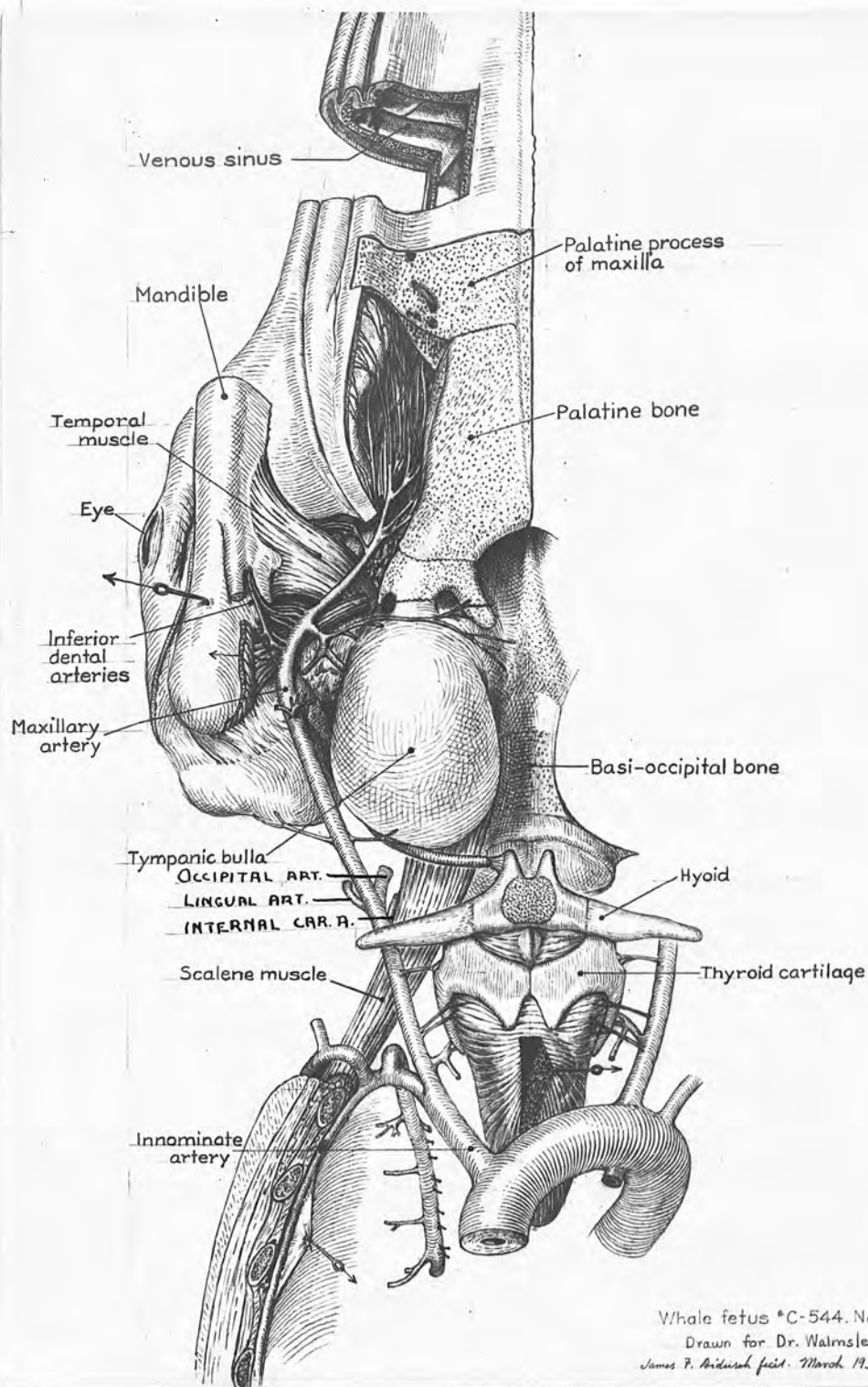
THE ARTERIES AND SOME OF THE VEINS  
OF THE HEAD AND NECK.

The right common carotid artery begins just in front of the level of the first costal cartilage and terminates under cover of the greater cornu of the hyoid bone by dividing into an internal and an external carotid artery. At its commencement it is 5 mm. wide and it has a total length of some 50 mm. It crosses the ventral surface of the scalenus medius from the medial to the lateral side but is separated from it by the vagus nerve and the sympathetic trunk. It lies deep to the sterno-thyroid and sterno-hyoid muscles and the internal jugular vein is on its lateral side. The adjacent fasciae were not arranged in the form of a tubular sheath.

The left common carotid and left subclavian arteries have an intra-thoracic course of about 25 mm. (for origin see page 69 ). They have the usual relationship to the phrenic, vagus, and cardiac nerves and are closely related to the thymus and thyroid glands.

In /





**Fig. 32 . Branches of the common carotid artery.**

In its intra-thoracic course the left common carotid gives off two small branches to the thymus gland and a branch to the laryngeal sac.

Beyond the thorax the left common carotid and the left subclavian have a course and relations similar to the corresponding arteries of the right side.

In the neck each common <sup>carotid</sup> artery has the following branches.- (a) A superior thyroid artery arises near its commencement and passes medially to the upper pole of the thyroid gland. (b) Two small branches to the laryngeal sac. (c) A small internal laryngeal branch which pierces the dorsal part of the thyro-hyoid membrane. (d) Two small branches which arise deep to the hyoid bone and pass to the prevertebral muscles.

The internal carotid artery begins under cover of the greater cornu of the hyoid bone; at its commencement it has a diameter of 2 mm. It passes forward along the lateral border of the scalenus muscle, but on account of the plane of the anterior cut and the subsequent retraction of the ends of the vessel further data on this part of its course could not be established. In the anterior section of the foetus the vessel was sought and found in the roof of the tympanic cavity. It was traced backwards as far as the basi-paroccipital fissure but anteriorly it could only be followed as far/

as the anterior part of the cavity where it became extremely small and thread-like.

The latter part of the course of the internal carotid artery was established only through the knowledge of the descriptions of Beauregard (1894) for *Delphis delphis* and *Balaenoptera acutorostrata*, Boenninghaus (1903) for *Phocaena phocaena*, Schreiber (1916) for *Globicephalus melas* and Slijper (1936) for *Phocaena phocaena*. Each of these authors describes the vessel as arising from either the innominate or the common carotid artery, passing through the basi-paroccipital fissure and the fenestra rotunda, traversing the tympanic cavity and then passing through the carotid canal into the cranial cavity where it terminates in arterial rete at the side of the hypophysis.

Since Sharpey (1835) first drew attention to the smallness of the internal carotid in adult Cetacea, it has been repeatedly demonstrated that this channel can have little, if any, functional significance in the post-foetal life. The obliteration of the internal carotid artery in its passage through the tympanic cavity is common to all Cetacea, though the relative age at which this takes place seems to vary. Schulte (1916) in his description of a 375 mm. foetal *Balaenoptera borealis* states that the lumen of the internal/

internal carotid is very narrow, and in my 580 mm. specimen (where I found the course of the artery to be as described) I found the lumen of the vessel to be obliterated in the anterior part of the tympanic cavity. Jackson (1845), however, in his description of a full-time specimen of *Delphinus* states that the internal carotid was wider than the external.

It is of interest to notice two further descriptions of the internal carotid in *Balaenoptera*.

Turner (1870) in a description of a nineteen and a half feet long foetal *Balaenoptera sibbaldii* describes the common carotid artery as dividing six inches from the aorta into a cervico-facial artery and a smaller branch that "was apparently the internal carotid". Turner does not, however, give any details regarding either the extra-or intra-cranial course of the internal branch.

Carte and Macallister (1871) in their description of a young *Balaenoptera rostrata* state that "The internal carotid, which formed part of the before mentioned plexus<sup>\*</sup>, continuing its course into the cranial cavity to supply the brain through the medium of its rete mirabile, where its inosculating branches interlaced with those of the venous plexus at the base of the skull".

The/

\* This is a reference to pterygoid plexus, page 93 .



The external carotid artery (the cervico-facial artery of Turner) is, in reality, the continuation of the common carotid artery after it has given off the small internal carotid branch. It runs forwards deep to the depressor mandibulae and sterno-mastoid and superficial to the hyoglossus muscle, and, as it passes deep to the mandible becomes continuous with the maxillary artery.

Branches.- (1) The occipital artery passes dorsally under cover of the sterno-mandibularis and trachelo-mastoid, and superficial to rectus capitis lateralis; under cover of the splenius it breaks into a series of branches which are distributed to the muscles of that region.

(2) The lingual artery is <sup>a</sup>relatively large trunk <sub>A</sub> which arises from the external carotid at the same level as the occipital artery. It passes along the lateral side of the genio-glossus muscle under cover of the hyoglossus and gives off early in its course numerous branches to the tissues of the intermandibular region and branches to the muscles of the tongue. One of its branches proceeds to the tip of the tongue maintaining a position lateral to the hypoglossus.

The hypoglossal nerve, as it passes ventrally, hooks around the occipital artery, then lies superficial to the external carotid artery and as it passes towards/

towards the tongue it lies ventral to the lingual artery but in the same fascial plane.

(3) The facial artery arises a little behind the mandible. It is a relatively small branch which passes ventrally between the sterno-mandibularis and genioglossus, and ends in a leash of exceedingly fine twigs that pass onwards close to the body of the mandible supplying the adjacent tissues. Several of these twigs pass around the lower border of the mandible and are distributed to the tissues in the region of the angle of the mouth and the eye. They are accompanied by a great plexus of thin-walled veins which form a surprisingly small trunk which enters the jugular vein.

(4) A small branch to the tympanic bulla arises at the same level as the facial artery. It passes medially ventral to rectus lateralis and terminates in a leash of branches on the surface of the bulla.

The maxillary artery is the continuation of the external carotid. It passes forwards deep to the mandible and superficial to the medial pterygoid muscle and the tympanic bulla, crossing below the lateral pterygoid from the medial to the lateral side. It then lies directly medial to the temporalis muscle, and leaving its anterior border it crosses above the posterior free border of the palatine process of the maxillary/

maxillary bone near its junction with the palatine bone. There it breaks into a leash of branches which pass forwards in the fibrous wall of the venous sinuses; some of them pass ventrally through the deficiencies in the hard palate and enter the palatal mucous membrane; (I was unable to detect the rudiments of either teeth or baleen in the upper jaw).

The venous sinuses are essentially foetal structures, as the corresponding region in the adult is

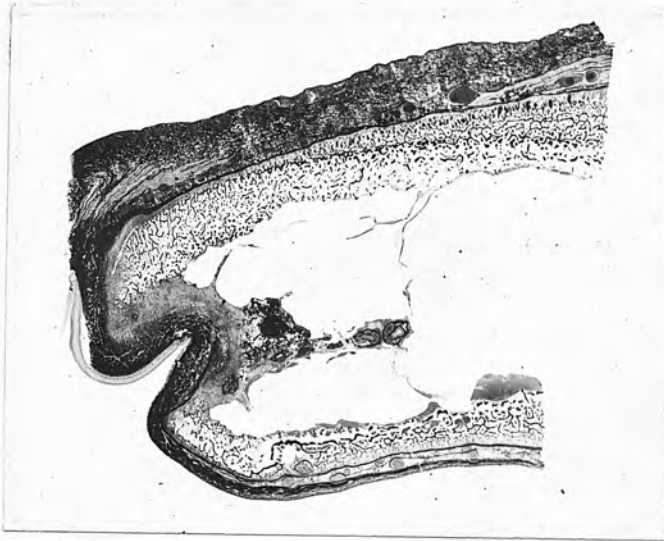


Fig. 33 . Transverse section of the maxilla to show the venous sinuses.

occupied by a firm, yellow homogeneous fatty substance containing many vessels. The palatine process of the adult maxilla also has numerous foramina; they transmit the vessels and nerves destined for the supply of/  
of/

the of<sub>^</sub>palatal mucous membrane and the baleen plates. The sinuses can therefore be looked on as a vascular mechanism which is associated with the rapid growth of baleen in the latter part of ~~the~~ gestation.

Pterygoid Venous Plexus (Basiscranial Rete).— The part of the maxillary artery that lies behind the palate is embedded in a dense venous plexus. This plexus, which is invested with a glistening membrane, lies dorsal to the medial pterygoid muscle and extends upwards to the base of the skull. Carte and Macallister (1871), and Ommanney (1932a) have described this plexus as being composed of both arteries and veins. Microscopic sections however, show it to be formed almost entirely of exceedingly thin-walled venous channels which are filled with



Fig. 34 . Photomicrograph of pterygoid veous plexus showing two large veins. Inside the lower vein there is a small muscular artery.



blood. The arteries in the plexus are relatively few and are merely the branches of the maxillary artery destined for the supply of the adjacent muscles. The position of the majority of the arteries is however singular, and as far as I am aware peculiar to this plexus, as they lie actually within the venous channels. I regard this plexus, therefore, not as a structure peculiar to the Cetacea, but as an accen-  
tuation of the venous plexus that is normally found in relation to the pterygoid muscles.

The maxillary vein (jugular vein of Carte and Macallister) commences by the union of the venae comitantes of the terminal branches of the maxillary artery and passes backwards lateral to the maxillary artery and unites with the internal jugular vein.

The pterygoid plexus sends numerous tributaries to the maxillary vein and in addition it is connected with the ophthalmic veins and with the intracranial veins by an emissary vein that passes through the foramen ovale.

#### Branches.-

The maxillary artery has the following branches.-

(1) Numerous branches are given to the adjacent muscles. These branches divide into fine stems as they traverse the pterygoid venous plexus and often lie within a vein, in other instances the artery has five/

five to ten veins around it. (2) Seven inferior dental arteries arise close together in linear formation. They pass ventrally to the mandibular foramen and traverse the canal in which they give off branches to the labium. Each artery is surrounded by several veins which open into the pterygoid plexus (Fig. 35 ). In the adult finback the arrangement of the inferior dental arteries is essentially similar to the foetus and in one specimen in which the mandible was cut transversely near its middle there were ten arteries and their accompanying veins in the mandibular canal (Fig. 36 ). (3) Arising at the same level as the inferior dentals there is an artery 3 mm. in diameter (a. pterygoideo-palatine of Boenninghaus, 1903), which passes medial to the lateral pterygoid muscle where it divides into three equally sized branches: (a) a palatine branch of the soft palate, (b) a tympanic branch which passes into the tympanic antrum, and (c) a branch which passes forward on the medial side of the lateral pterygoid muscle and the maxillary artery and enters the temporal muscle; some of the terminal branches of this stem pierce the anterior border of the muscle and enter the labium of the lower jaw.

(4) A superficial temporal branch arises at the anterior border of the temporal muscle. It passes around/

around the anterior border of the muscle and ascends on its superficial surface deep to the zygomatic arch whence its branches turn forwards on the dorsum of the snout where they break into a leash of exceedingly fine twigs.

(5) Small branches which communicate with the ophthalmic arteries.

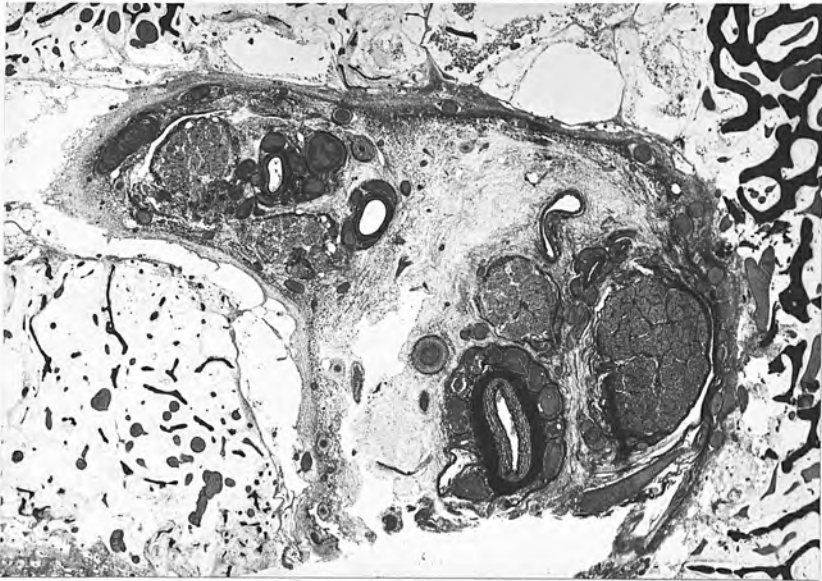


Fig. 35 . Transverse section of mandible to show multiple vessels in mandibular canal



Fig. 36 . Block of inferior dental vessels of adult finback whale.

## THE THORACIC AND ABDOMINAL PARTS

### OF THE DESCENDING AORTA

In this section the arteries and veins of the organs have been described together.

The thoracic part of the descending aorta extends from the fifth to the fifteenth thoracic vertebra and at that level passes through the diaphragm to become the abdominal aorta. It is 150 mm. long and has a maximum width of 15 mm., decreasing in size from before backwards. It is embedded in dense areolar tissue which blends with the ventral longitudinal ligament of the vertebral column. Ventrally the aorta is related to the oesophagus - which separates it from the root of the left lung - the pericardium and the diaphragm.

The thoracic aorta has the following branches.

- (1) Several small oesophageal branches.
  - (2) Ten pairs of intercostal arteries supply the fifth to the fourteenth intercostal spaces. It is of interest to note that the arteries of the right and left sides are given off separately; the lumbar segmentals, on the other hand, arise by a common trunk.
- Each /

Each vessel is about 2 mm. in diameter. It passes dorsally in contact with the intervertebral fibrocartilage deep to the sympathetic trunk and at the level of the transverse processes gives off a large dorsal branch; it then turns laterally and enters the inters the intercostal space. As the artery traverses the space it occupies the typical morphological position of that vessel and has the usual branches; it anastomoses with the arteries of the ventral part of the space but does not break up into a leash of branches, as has frequently been described. It is accompanied by a plexus of veins which unite in the dorsal part of the space to form a single trunk which joins the spinal vein.

The dorsal branch ramifies in the substance of the epaxial muscles and gives off a spinal branch.

The abdominal aorta lies in the median plane and extends from the last (15th) thoracic vertebra to the intervertebral disc between the fourteenth and fifteenth lumbar vertebrae, where it terminates by dividing into a right and a left common iliac artery and a caudal artery. It has an average diameter of 10 mm.

As the aorta passes backwards it gradually recedes from the vertebral column and its terminal part is 25 mm. from it. It lies between the right and left hypaxial /



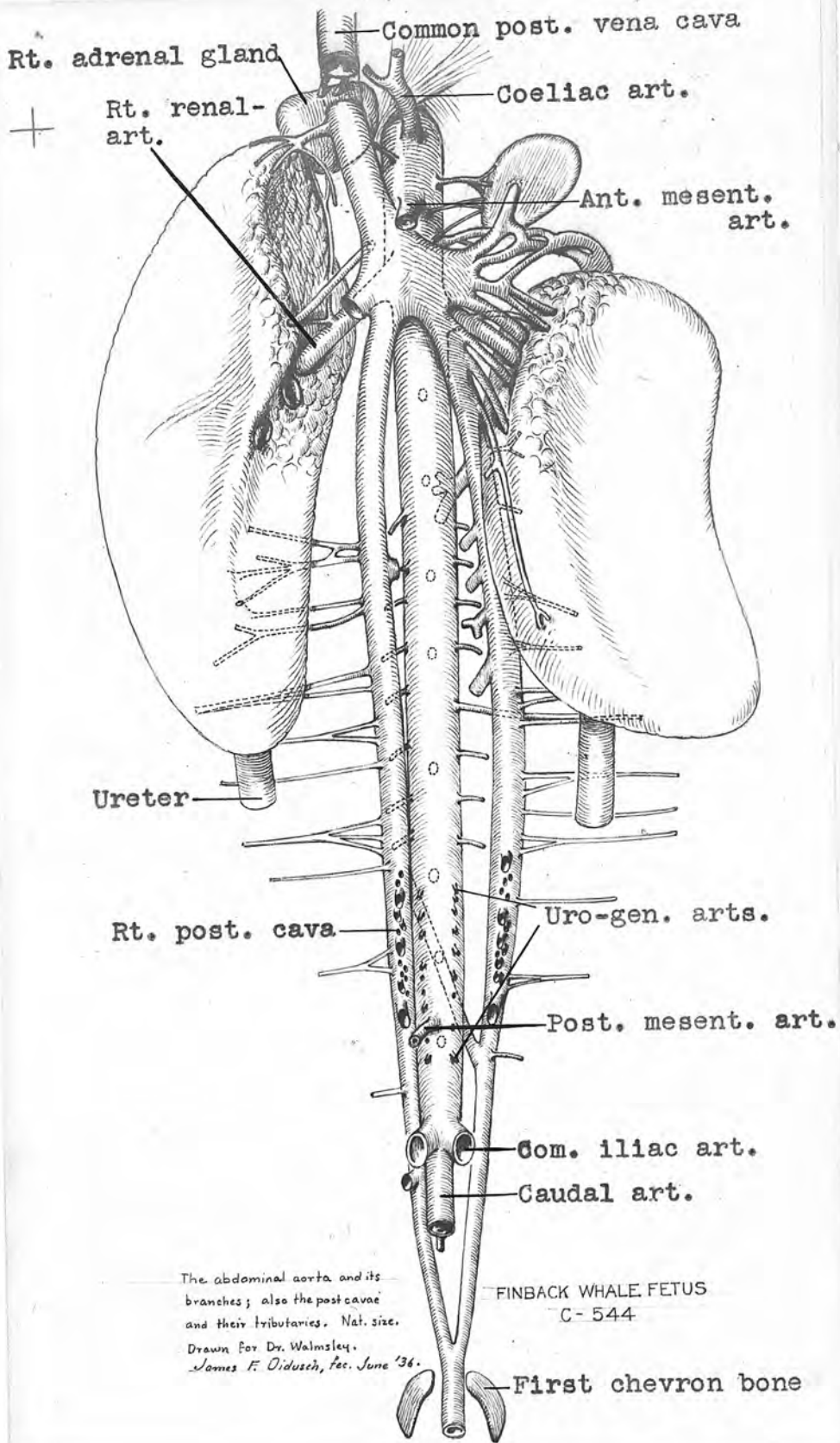


Fig. 37. The abdominal aorta and its branches.

hypaxial muscles, but as far forwards as the anterior pole of the left kidney it is separated from them by the right and left postcavae. (In the preserved foetus the relationship of the artery to the hypaxial muscles and its distance from the vertebral column are largely dependent on the position of the foetus during its fixation.)

The post-umbilical part of the abdominal cavity is small and all the viscera, with the exception of the genital organs, the bladder, and the terminal part of the large intestine lie anterior to the umbilicus. The most important of the ventral relations of the aorta are the coeliac plexus, the gastro-splenic artery which separates it from the pancreas (the gastro-splenic vein is embedded in the dorsal part of the pancreas), the superior mesenteric vein, the third part of the duodenum, the left postcava, and coils of small intestine.

Branches.— The unpaired visceral branches are the coeliac, anterior mesenteric, and posterior mesenteric; the paired visceral are the suprarenals, the renals, and the genito-urinaries.

The parietal branches are the lumbar segmental arteries which arise as single branches (cf. inter-costal branches), the right and left common iliac arteries, and the caudal artery.

The/

The coeliac artery arises from the aorta immediately behind the aortic opening in the diaphragm; this opening is 16 mm. posterior to the oesophageal opening. The coeliac artery is 3 mm. wide and divides 16 mm. from its origin into a small hepatic branch and a gastro-splenic branch.

(1) The hepatic artery is notable for its small size. It passes cranially and to the right behind the pancreas and turns round the left border of the portal vein to gain its ventral side on which it proceeds to the porta hepatis. During its course the artery lies behind the peritoneum of the greater sac and not within the lesser omentum. Its only extra-hepatic branch is a small right gastric artery.

(There is no gall-bladder in *Balaenoptera physalus*).

(2) The gastro-splenic artery passes forwards and to the left for 30 mm. and then divides into a gastric and a splenic branch; in the greater part of its course it lies dorsal to the pancreas. (a) The splenic branch traverses the gastro-phrenic ligament and passes along the greater curvature of the first compartment of the stomach to the spleen; it gives off several branches to the first compartment. (b) The gastric branch continues forward, first on the dorsal abdominal wall, then in the gastric-phrenic ligament, and enters the deep dorsal fissure between the first and second/

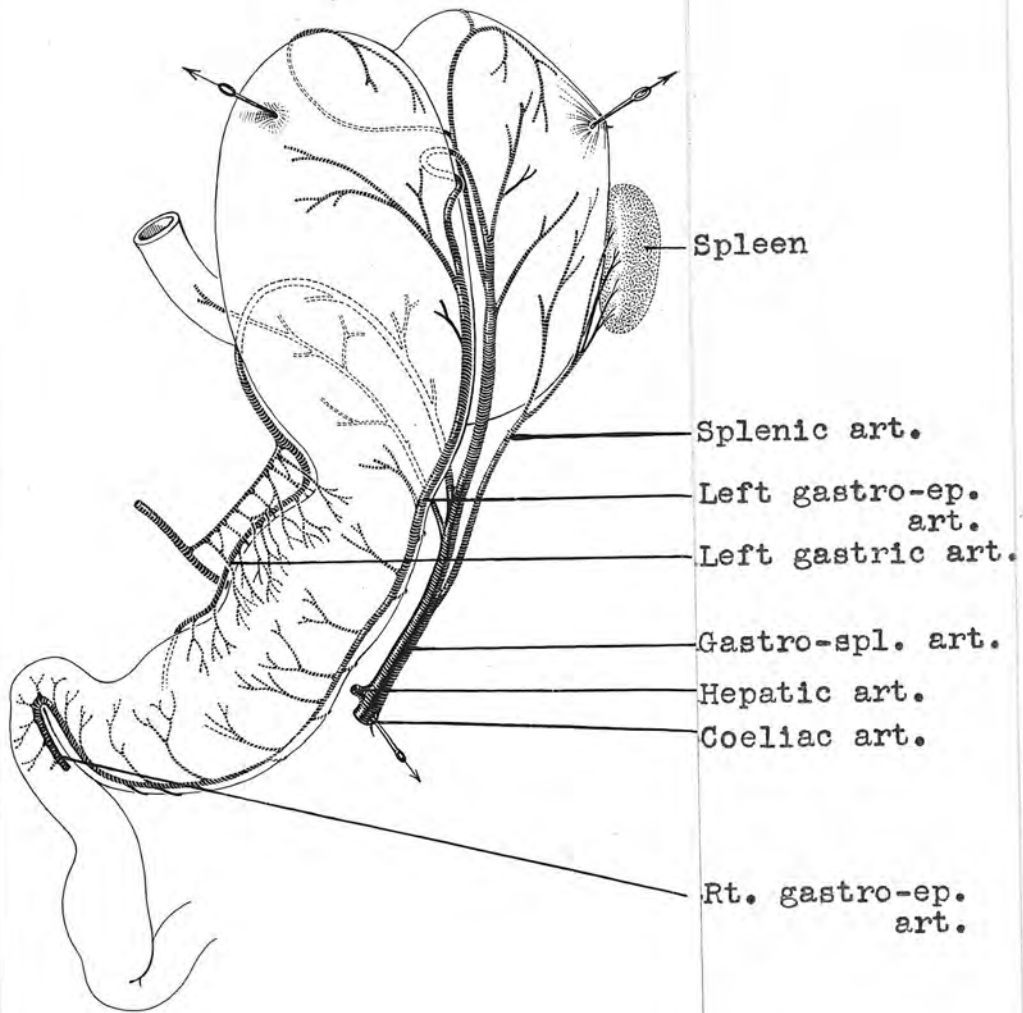


Fig. 38 . The arteries of the stomach. The hepatic branch of the coeliac artery is cut near its origin and the coeliac artery is displaced backwards. The first gastric compartment is retracted to the left and the second compartment is retracted to the right.

second compartments of the stomach. In figure 38 to which frequent reference is essential in order to appreciate the course of the gastric vessels, the first compartment of the stomach has been strongly retracted to the left and the second compartment to the right. This has disturbed the normal contour of the viscus, and gives the deep dorsal fissure between the first and second gastric compartments the appearance of being on the left side.

At the posterior end of the fissure the gastric branch divides into a left gastric and left gastro-epiploic. The left gastric passes forwards dorsal to the second compartment to reach the lesser curvature, on which it passes to the right as far as the fourth gastric compartment. It gives off a branch that passes to the right to anastomose with the gastric branch of the hepatic; this combined trunk gives off numerous branches to the ventral and dorsal surfaces of the third compartment. The gastro-epiploic branch passes deeply into the dorsal fissure and curves ventrally till it gains the greater curvature of the second compartment, it then passes to the right and effects an anastomosis with the right gastro-epiploic branch which comes from the anterior mesenteric artery.

In addition to the multiple twigs which arise from the main branches of the gastro-splenic artery, an oesophageal/



oesophageal branch arises from the gastric artery and passes along the right border of the first gastric compartment to the oesophagus; it gives numerous branches to the cardia.

The anterior mesenteric artery arises from the ventral side of the aorta 14 mm. behind the coeliac artery; at its origin it has a diameter of 4 mm. The closeness of origin of these two visceral stems has frequently been referred to and Carte and Macallister (1871) in a specimen of *Balaenoptera rostrata*, found the two vessels arising by a common trunk. The commencement of the anterior mesenteric artery is immediately in front of the terminal transverse part of the left post cava (Fig. 37 ) and as it passes backwards it lies ventral to the vein. The artery then crosses the junction of the third and fourth parts of the duodenum and passes backwards medial to the ascending colon. In this part of its course the artery is embedded in a thick cord of nerves, outside of which there are two veins, one lying between the artery and the colon; they unite in the region of the duodenum to form a single stem.

After a close examination of Specimen 46 of *Balaenoptera sibbaldi* in Edinburgh University Anatomical Museum I am convinced that the portion of the intestine there preserved is a part of the ascending colon and that/



Fig. 39 . Transverse section of the ascending colon. The anterior mesenteric artery is surrounded by nerves.

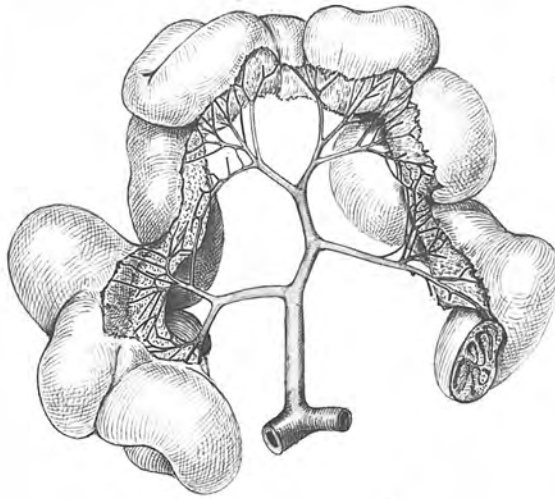


Fig. 40 . Transverse section of branches of anterior mesenteric vessels of adult finback. The vein is thick-walled and has much elastic tissue in the outer part of its wall. In this figure the vein lies above the artery.

that the "moniliiform tube" of Turner is a part of the main trunk of the anterior mesenteric artery. Turner (1870) described this moniliiform tube as lying along the entire length of the mesenteric attachment of the gut, and extending back along the rectum. In my examination of several specimens of adult humpback, finback, and sperm whales I was unable to discover anything comparable to this moniliiform tube, although I was much impressed by the large and numerous lymph glands - often arranged in "chain-like" formation - which lay close to the mesenteric border of the gut.

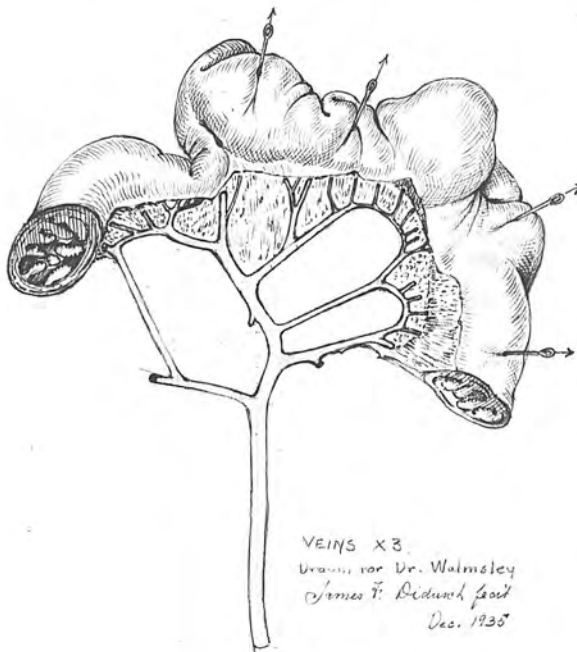
The main continuation of the anterior mesenteric artery passes behind the caecum and is distributed to the terminal part of the ileum where it effects anastomoses with the distal ileal branches which are given off near the root of the artery.

Branches. - (1) A pancreatico-duodenal branch is given off immediately prior to the main trunk crossing the duodenum. This vessel is 3 mm. in diameter and passes to the right through a vascular cleft in the head of pancreas to meet the duodenum at the junction of its second and third parts. From there the artery continues proximally between the head of the pancreas and the duodenum, giving branches to both. It then follows the greater curvature of the stomach as far as its third compartment where it anastomoses with the left/



BIOLOGY and ART  
 PHILADELPHIA, PA., X3  
 Drawn for Dr. Walsley, James T. Biduch, fecit (Artycus) Mid-jejunol. Dec. 1935.

Fig. 41 . Loop of jejunum with branch  
 of anterior mesenteric artery.



VEINS X3  
 WALSLEY  
 James T. Biduch, fecit  
 Dec. 1935

Fig. 42 . Loop of jejunum with its  
 veins.

left gastro-epiploic; in the last part of its course it may be termed the right gastro-epiploic. A single vein accompanies the artery and drains an area similar to that supplied by the artery. (2) A leash of jejunal and ileal branches arise as the main trunk crosses the duodenum and these immediately enter the mesentery\*.

The distribution of the arteries is noteworthy in the absence of arterial arcades.

(2) A left colic branch is given off at the same level as the (2); it passes distally closely applied to the medial side of the descending colon and anastomoses with the posterior mesenteric artery at the level of the middle of the left kidney.

(4) Numerous branches are given to the ascending colon by the main trunk.

The posterior mesenteric artery arises from the aorta/

\* The parietal attachment of the mesentery is exceedingly short - being only about 40mm. It is almost in the median plane and lies between the ascending colon on the right side and the ascending portion of the duodenum on the left side. The mesentery in addition to suspending the jejunum and ileum from the posterior wall also encloses the part of the ascending colon that lies distal to the transverse part of the duodenum - this part of the colon being exceedingly mobile. The anterior mesenteric vessels, after they have crossed the transverse part of the duodenum, run in close relationship with the left side of the ascending colon. Throughout their entire course the vessels are accompanied by a great network of sympathetic nerves.



aorta 30 mm. anterior to its termination; at its origin it is 2 mm. in diameter. It enters the mesocolon which suspends the posterior part of the descending colon from the dorsal abdominal wall, and within it, passes ventrally and backwards for 20 mm; it then divides into an anterior and a posterior branch.

The anterior branch passes forward in close relationship with the descending colon and effects an anastomosis with a colic branch of the anterior mesenteric in the region of the colic flexure; it distributes branches to the colon in a typical manner. Its accompanying vein increases in size as it is traced forwards and enters the anterior mesenteric vein at the same level as the pancreatico-duodenal vein.

The posterior branch passes backwards close to the colon and 100 mm. in front of the anal canal divides into right and left branches which almost immediately enter the colon submucosa. I was unable to demonstrate any anastomoses between this branch and the posterior rectal artery.

### THE ADRENAL VESSELS.

Arteries.— The left adrenal gland is supplied by three arteries which arise directly from the aorta. The anterior artery is the largest and arises from the ventral surface of the aorta mid-way between the coeliac and the anterior mesenteric artery. The middle vessel arises at the side of the anterior mesenteric artery and the posterior arises just medial to the origin of the left renal. The arteries enter the medial border of the gland.

The right adrenal gland is also supplied by three arteries, but on this side, only the anterior artery arises from the aorta; it does so a little behind the coeliac artery. The middle artery arises from the root of the renal artery and passes forwards dorsal to the right postcava, and the posterior artery arises from the anterior branch of the renal.

Veins:— The left adrenal gland is drained by a single large vein which leaves the ventral surface of the gland and passes backwards to join the plexus of renal veins.

The right adrenal gland is drained by two small trunks which leave its ventral surface near its anterior end and open directly into the common posterior cava which lies directly ventral to the gland.

THE RENAL VESSELS.

Arteries.- The right renal artery arises from the aorta 16 mm. behind the anterior mesenteric artery; it has a diameter of 6 mm. At its origin it lies dorsal to the commencement of the common posterior cava and it passes obliquely backwards and to the right for 20 mm., dorsal to the right renal vein, and enters the hilum of the kidney 35 mm. behind the anterior pole. It gives off a small anterior renal branch 7 mm. from its origin which enters the hilum 10 mm. in front of the main trunk; this branch gives off the posterior adrenal artery. The main trunk runs backwards in the central fibrous tissue core and terminates in two fine twigs which ramify on the ureter as it leaves the posterior pole (Fig. 43). During its backward course the artery lies about midway between the medial and lateral borders of the kidney and throughout its whole extent gives off at the right angles medial and lateral branches. These branches pass from the main trunk in fibrous tissue septa which separate the adjacent lobes of the kidney, and they terminate some distance from the kidney surface by dividing into twigs which pass to the renculi. The main arterial trunk is accompanied by venous channels that/

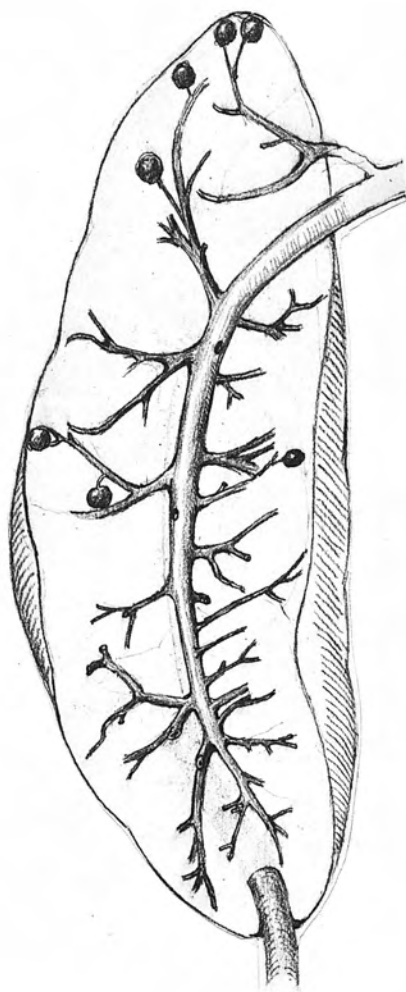


Fig. 43 . The right renal artery and its branches. A few twigs are shown going to the renculi and the ureter is seen leaving the lower pole of the kidney.

that form numerous anastomoses around the artery.

The left renal artery arises 28 mm. behind the anterior mesenteric artery and has a diameter of 5 mm. At its origin it is dorsal to the trunk formed by the left renal vein and the left posterior cava. It passes backwards and to the left for 20 mm. and enters the hilum of the kidney 35 mm. behind the anterior pole. It gives off a small anterior branch 5 mm. from its origin which runs forwards and to the left dorsal to the renal veins, to enter the hilum 10 mm. anterior to the main trunk. Within the hilum of the kidney the left artery has a course and distribution similar to right renal artery.

Veins.— The renal veins, in contrast to the arteries, are multiple on each side, and are divisible into peripheral and central groups (Fig. 44). The central veins drain all but <sup>the</sup> more peripheral renculi and they have frequent anastomoses with one another; the anastomatic channels in many instances embrace the main arterial trunk. The peripheral veins form an intricate network which lies within the serous covering of the kidney. The veins lie between the superficial renculi and drain directly into the posterior cavae by small transverse channels; they also have numerous anastomoses with the central veins.

On the right side one large vein leaves the hilum ventral/



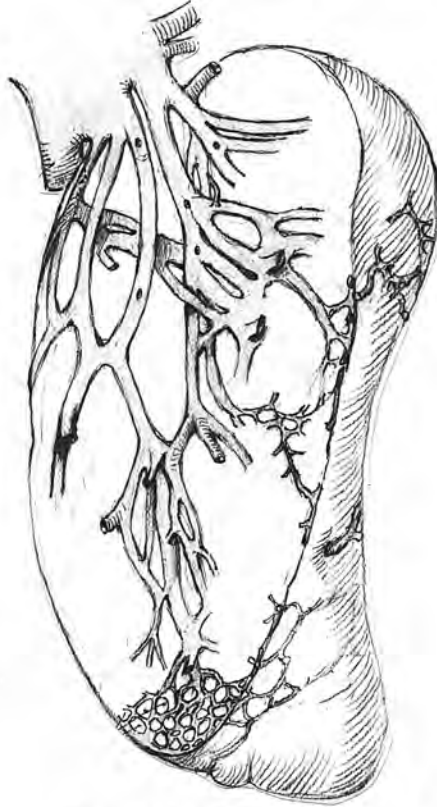


Fig. 44 . The veins of the left kidney.  
The central veins form an irregular plexus within the kidney.

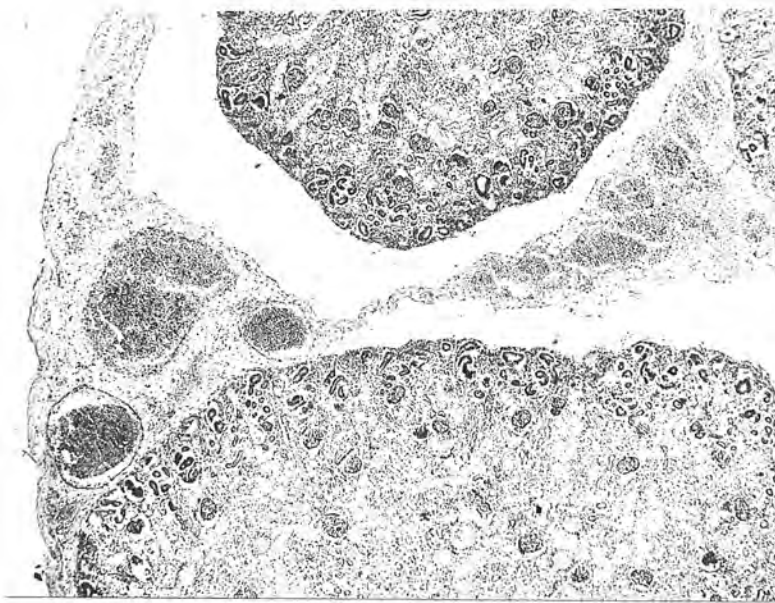


Fig. 45 . Photomicrograph of kidney, (X45).  
Parts of two peripheral renculi with the  
intervening peripheral veins are shown.

ventral to the renal artery and passes forwards and medially and joins the commencement of the common posterior cava. In addition, there are numerous small veins which pass medially from the peripheral plexus; the anterior of them join the common caval trunk and the posterior join the right posterior cava.

On the left side three central veins emerge from the anterior end of the hilum ventral to the artery; each vein is about 4 mm. in diameter. The posterior vein enters the left posterior cava directly while the two anterior veins join the anterior peripheral veins and the adrenal vein to form a common trunk which unites with the left posterior cava as it passes ventral to the aorta to join the right posterior cava. Closely associated with the central trunks are numerous peripheral veins which in most cases join the common trunk; four small peripheral veins leave the dorsal surface of the kidney and drain directly into the left posterior cava.

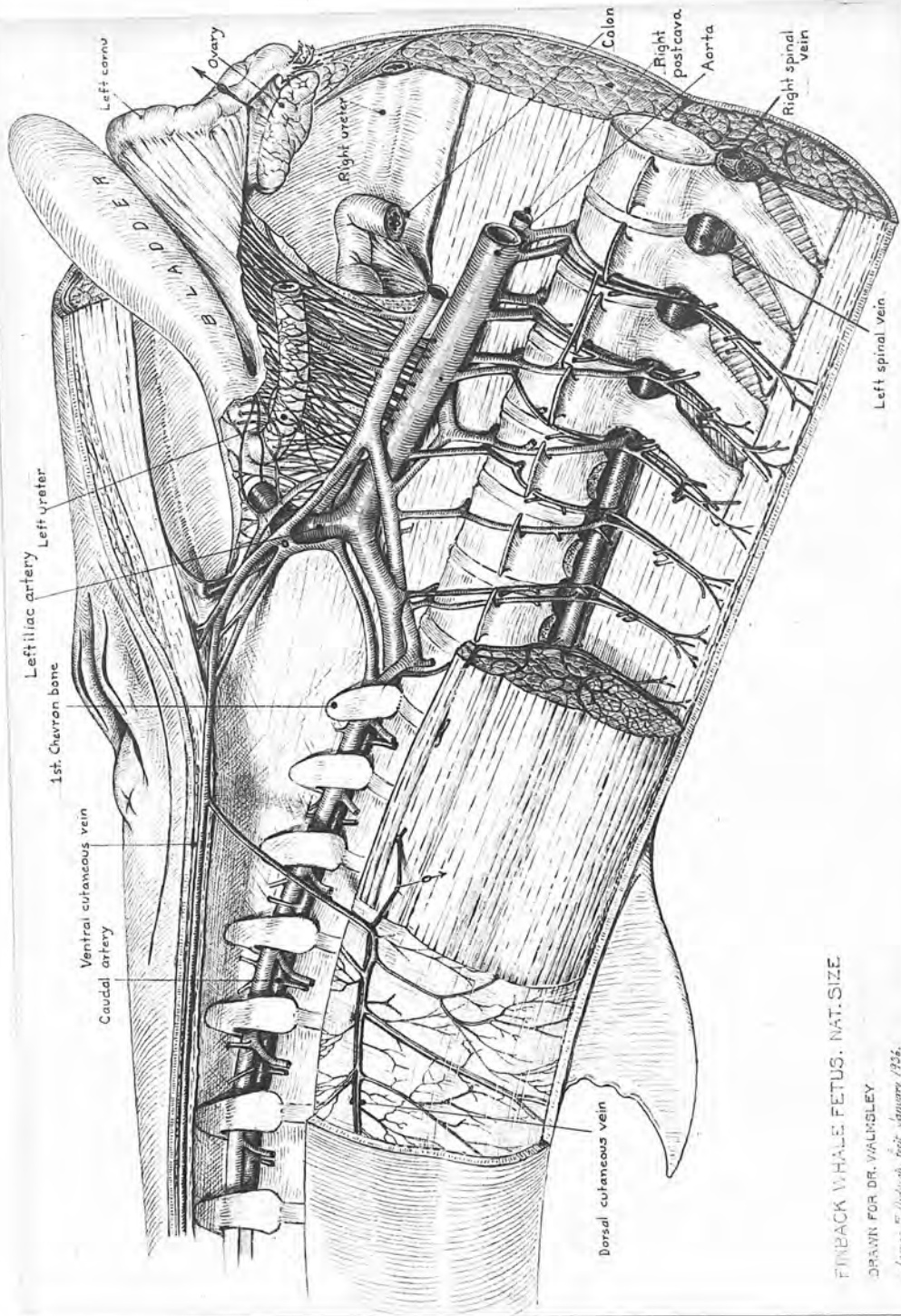
THE UROGENITAL VESSELS.

Arteries.— Ten urogenital arteries take origin in linear series from the ventral surface of the aorta 5 mm. from the middle line. They are spaced about 5 mm. from one another, the most posterior arising about 20 mm. in front of the termination of the aorta; they have, on the average, a width of 2 mm. In the first part of their course they pass ventrally and slightly laterally and here they lie medial to the posterior cava of the corresponding side (Fig. 46).

The seven anterior vessels enter the broad ligament at its attachment to the dorsal pelvic wall and as they do so lie on the medial side of the ureter; each vessel here divides into several branches. Within the broad ligament the vessels continue to divide and radiating in a fan-like manner are distributed to the entire genital tract from the ovary to the vagina.

The three posterior vessels pass ventral to the vagina and the neck of the bladder where each divides into several branches. Some of these branches pass forward and supply the ureter and the bladder and others pass backwards and supply the vagina and the urethra.

Veins.—/



FINBACK WHALE FETUS. NAT. SIZE.  
 DRAWN FOR DR. WALMSLEY  
 James F. Gidycz, *Art. January 1926.*

Fig. 46. Side view of pelvis after removal of left lateral wall. The foetus is lying on its dorsal side. The uro-genital vessels are shown lying in the broad ligament.

Veins.- Each urogenital artery is accompanied by two, three, or even four venae comitantes. The veins, unlike the arteries, have frequent anastomoses with one another (Fig. 47 ). The veins which drain the genital tract pass directly into the posterior cavae, whereas those from the bladder and the ureter pass to the pelvic venous plexus of which they form an integral part.

The urogenital arteries and veins which have been described entirely replace the uterine, ovarian, and vesical vessels commonly found in most mammals. Barkow (1866) in his magnificent atlas illustrates the blood supply of the genital organs in *Phocaena phocaena*. He there shows three arteries arising from the iliac as it lies in relation to the vagina. These vessels form a dense arterial plexus in the broad ligament out of which there arise multiple vessels which pass to the genital organs. Turner (1870) in his description of the urogenital tract of the adult *Orca gladiator* describes some twenty arteries lying between the layers of the broad ligament close to the side of the cervix uteri; these vessels are about the size of the human brachial or ulnar. Turner does not state from where they arise.

In foetus No.1 the broad ligament has an average thickness/



thickness of 5 mm. and in the most part is formed of the plexus of vessels.

In adult humpback (*Megaptera nodosa*) and finback whales the broad ligament is about 15mm. thick and has a similar plexus of vessels within it (Fig. 48); the arteries have an average diameter of 3mm. and the veins are thin-walled as in the foetus.

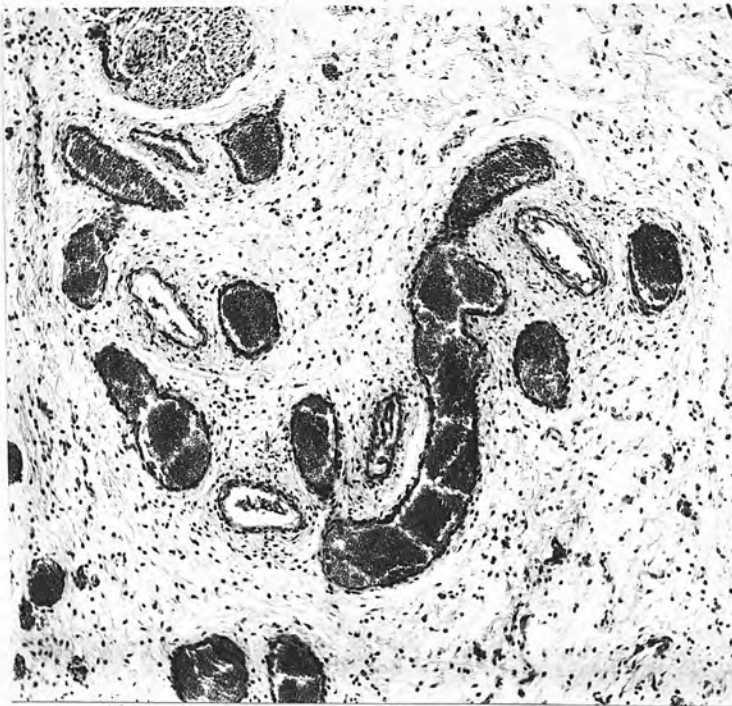


Fig. 47 . Section of broad ligament of foetus. An anastomosis between two veins is seen.

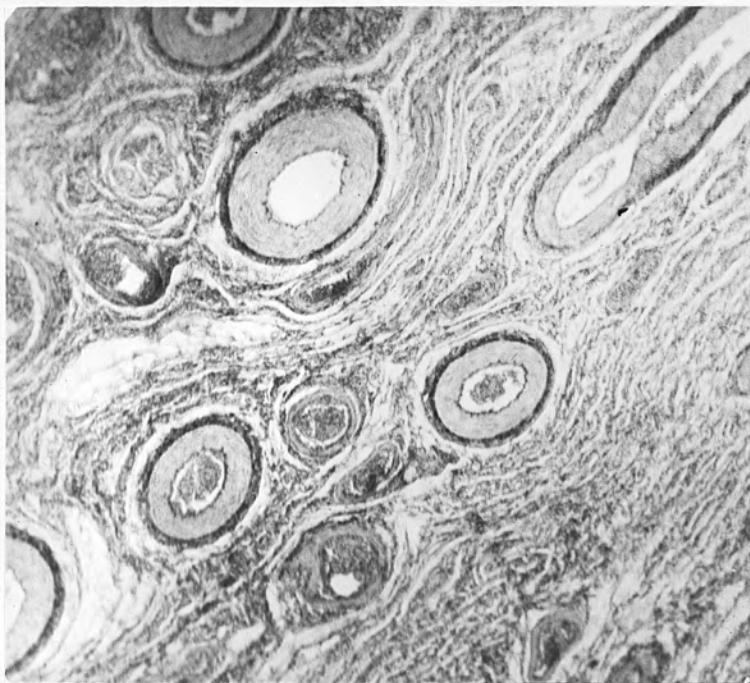


Fig. 48 . Section of broad ligament of  
adult finback whale

Parietal Branches

(1) A left posterior phrenic artery arises from the aorta at the same level as the coeliac. It supplies the dorsal part of the diaphragm. There is no corresponding branch on the right side.

(2) The lumbar arteries of the right and left sides take origin by common stems. They are in series with the vertebrae except for those corresponding to the eighth and fourteenth vertebrae which are absent. Each artery passes dorsally between the hypaxial muscles and divides on the ventral surface of the vertebral body into right and left branches. Each of these vessels gives off a large dorsal branch that supplies the epaxial muscle and then continues laterally between the epaxial and hypaxial muscles to be distributed in the usual manner to the lateral and ventral muscles of the abdominal wall.

TERMINAL BRANCHES OF AORTA

The aorta terminates at the level of the last lumbar vertebra by dividing into the two common iliacs and the caudal artery.

The caudal artery continues backwards and dorsally between the two hypaxial muscles and enters the haemal canal. The haemal canal is bounded ventrally by thirteen chevron bones and dorsally by the centra of the caudal vertebrae and the intervening fibro-cartilages; the canal is lined by a strong fibrous sheath which the segmental vessels pierce. It is worthy of note that the first chevron bone, which is the smaller than the second, has separate right and left halves whose ventral ends are separated by a distinct gap; this ensures a large anterior hiatus for the haemal canal. Within the canal the caudal artery is close to the vertebrae, which is in contrast to the position of the aorta in the lumbar region where the whole thickness of the hypaxial muscles separates the artery from the vertebrae. The caudal artery /

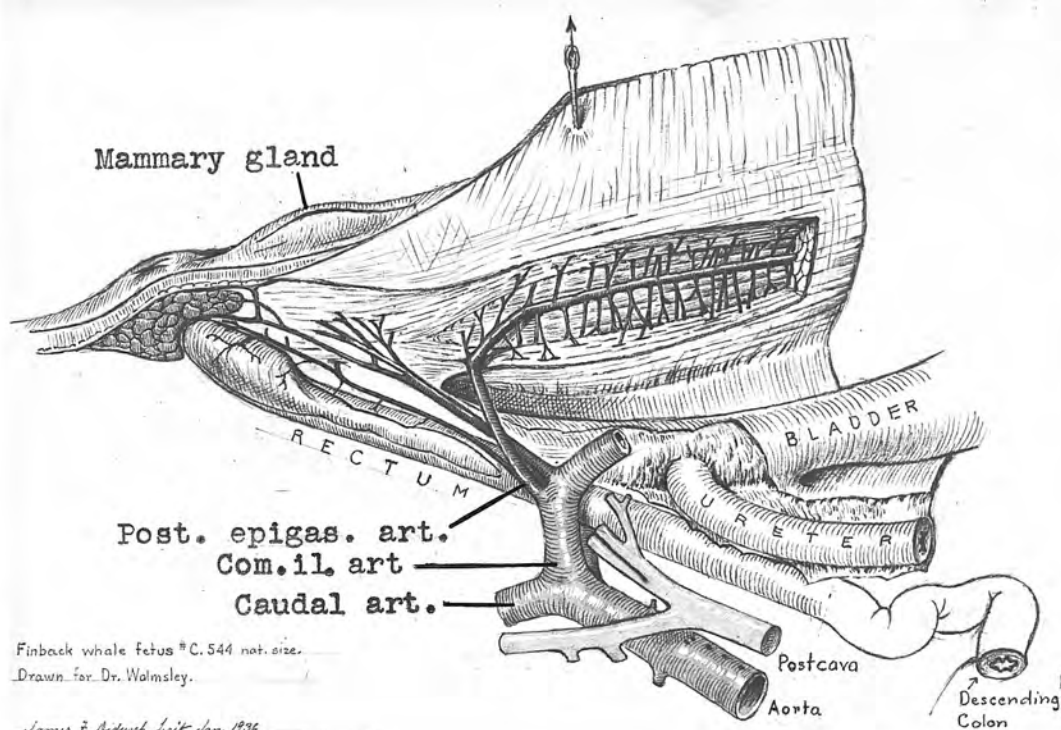


Fig. 49 . The terminal branches of the aorta and the branches of the common iliac artery.



artery continues backwards beyond the haemal canal to terminate on the ventral surface of the rudimentary vertebrae of the flukes.

Branches.- The segmental arteries of the right and left sides arise separately (cf. aortic segmentals) and have a typical muscular distribution (Fig. 46 ). Several single ventral branches ~~passing~~ pass downwards between the hypaxial muscles which they supply; numerous branches arise from the terminal portion of the artery and pass backwards and laterally in the substance of the flukes.

The caudal artery is accompanied throughout by the caudal vein.

Slijper (1936) states that in a 105 mm. foetal *Balaenoptera acutorostrata* the caudal artery is surrounded by an arterial plexus that originates from it. I did not find any evidence of this arterial plexus, which is in agreement with the findings of Delage (1885) in a foetal *Balaenoptera musculus*.

The caudal vein commences in the ventral surface of the vertebra of the flukes by the union of the several veins which drain them. The stem passes forward, at first between the hypaxial muscles and then within the haemal canal where it lies ventral to the caudal artery. At the anterior end of the haemal canal it divides into two trunks which pass downwards and /

and forwards to the aortic termination; one trunk lies dorsal to the caudal artery, the other lies ventral (Fig. 46 ). These vessels enter into a complicated anastomosis with the vessels that drain the pelvis and the subcutaneous tissues of the pedicle, and they together form a dense venous plexus. This plexus lies on the lateral sides of the vagina and I have deemed it advisable to term it the "pelvic" plexus rather than the "inguinal" plexus. (Ommanney 1932a). The tributaries of the caudal vein correspond to the branches of the caudal artery, there being in addition, however, the anastomotic channels to the spinal vein.

The superficial veins of the pedicle are represented by a ventral and a dorsal trunk on each side. They commence on the flukes and pass forward in a ventro-lateral and a dorso-lateral position respectively as far as the level of the anus, where the dorsal vein passes downwards to join the ventral vein. The common trunk that is formed passes inwards between the lateral and medial attachments of the rectus muscle and joins the pelvic plexus.

The common iliac artery.- Owing to the absence of an arterial stem to a posterior extremity the terminology that should be adopted for the terminal branches/

branches of the aorta has been a subject of much controversy. von Baer (1835), Barkow (1851) and Murie (1871) have all used the term "common iliac" but Cuvier (1805), Meckel (1831), Knauff (1905) and Slijper (1936) have referred <sup>to</sup><sub>Δ</sub> the two lateral terminal branches as the "hypogastrics".

The common iliac artery arises from the aorta and passes almost directly ventrally to the lateral side of the rectum, where it divides into the posterior epigastric and the umbilical artery (the hypogastric artery of Murie). The iliac artery and its branches are embedded in the pelvic venous plexus (p.139 ) and the venae comitantes that accompany these arteries terminate in the plexus.

The posterior epigastric artery is the smaller of the terminal branches; it runs ventrally to the abdominal wall and then passes forwards between the rectus abdominis and the thinned-out posterior margin of the transversus abdominis. Once within the sheath of the rectus it enters the substance of that muscle in which it passes forward almost to the costal margin; it gives numerous branches to the muscle throughout its course.

On the right side the posterior epigastric has two branches (a) a small middle rectal that supplies the rectum, vagina and urethra, and (b) a mammary that passes/

passes backwards a little ventral to the urethra and passes through the neuro-vascular foramen between the lateral and medial heads of origin of the rectus abdominis. The major part of the artery ends in the mammary gland, but a small branch is continued backwards to the external sphincter of the anus.

On the left side the mammary artery arises from the umbilical near its commencement.

Umbilical Arteries. In foetus No.1 the umbilical cord had been cut at its attachment to the abdominal wall and the intra-abdominal parts of the vessels had undergone considerable retraction. I was, however, able to examine the vessels and the cords in the other foetuses, and it is from the data there acquired that the following description is given.

Each umbilical artery passes forward to the umbilicus, first on the lateral and then on the dorsal side of the urachus. The two arteries and the urachus are enveloped in a common muscular sheath which is of considerable thickness. The arteries pass into the cord as separate stems and do not join to form a single stem as has been described for *Balaenoptera physalus* by Ommanney (1932 b) and for *Globiocephalus melas* by Murie (1874).

I was unable to demonstrate any vesical branches arising from the umbilical arteries, but Murie (1874) has/



Fig. 50 . Transverse section of the umbilical cord of foetus No. 1. The lumen of the allantois is seen between the two umbilical arteries.

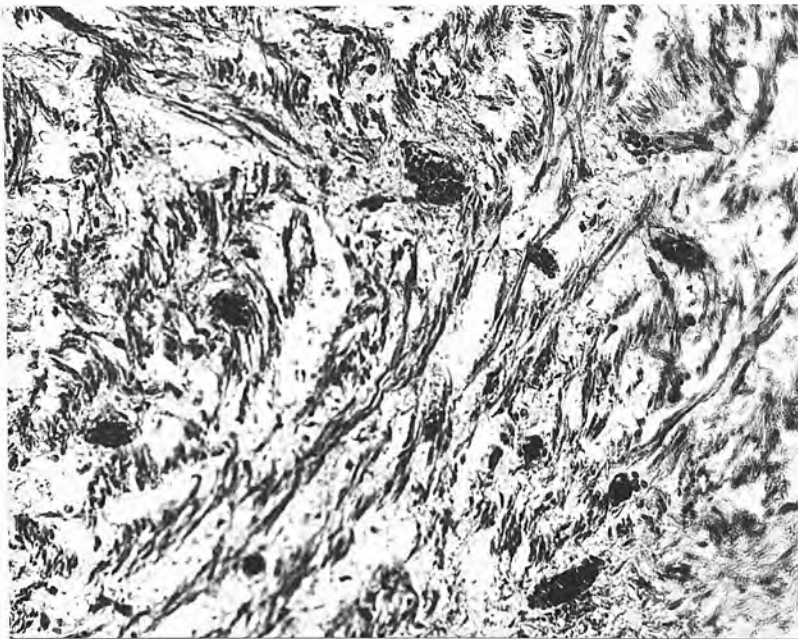


Fig. 51 . Part of the stroma of the umbilical cord (X150). The dark areas are the vasa propria which are filled with blood corpuscles.



has found them in *Globiocephalus melas* and Slijper (1936) found them arising from the proximal part of the umbilical trunk in adult *Phocaena phocaena*.

I have been unable to find any reference to the closure of the umbilical arteries in the Mysticeti, but the thick muscular sheath that is common to the urachus and the arteries would be a very powerful factor in their mechanical occlusion.

In the umbilical cord (Fig. 50 ) there are two umbilical arteries, two umbilical veins and the allantois. The two umbilical veins lie in the anterior part of the cord, and as they pass through the umbilical orifice they unite and form a single trunk. Scattered throughout the umbilical cord there are numerous small arteries and veins, the vasa propria, which Wislocki (1933) has described as being present in several mammals. Slijper (1936) states that the vasa propria are directly continuous with the plexus of the epigastric veins which pervades the rectus muscles.

VENOUS SYSTEM.

The venous system throughout the body is characterized by its great wealth of channels, a condition that is common to all Cetacea. Arteries in many places are embedded in a network of accompanying veins, and in other situations, such as the pelvis, the pterygoid region, and the submucosa of the soft palate the veins form dense independent plexuses. It seems, however, that there is much variation, in the extent to which the venous plexuses are developed in the various Cetacea, as I have not met with any so marked, or so generalised, as for example, have been described and figured by von Baer (1835) in the *Delphinus phocaena* and by Murie (1874) in *Globiocephalus melas*. One feature of the plexuses and the networks of veins, is the small outlet afforded them by their proximal channels, and this explains why that in all cases where microscopical examination of the venous plexuses was made, the vessels were found to be filled with blood.

The venous vascularity of the muscles is equally apparent in microscopical sections of foetal tissues and in the naked eye observation of adults during dismemberment.

The walls of the veins, quite independent of the size/

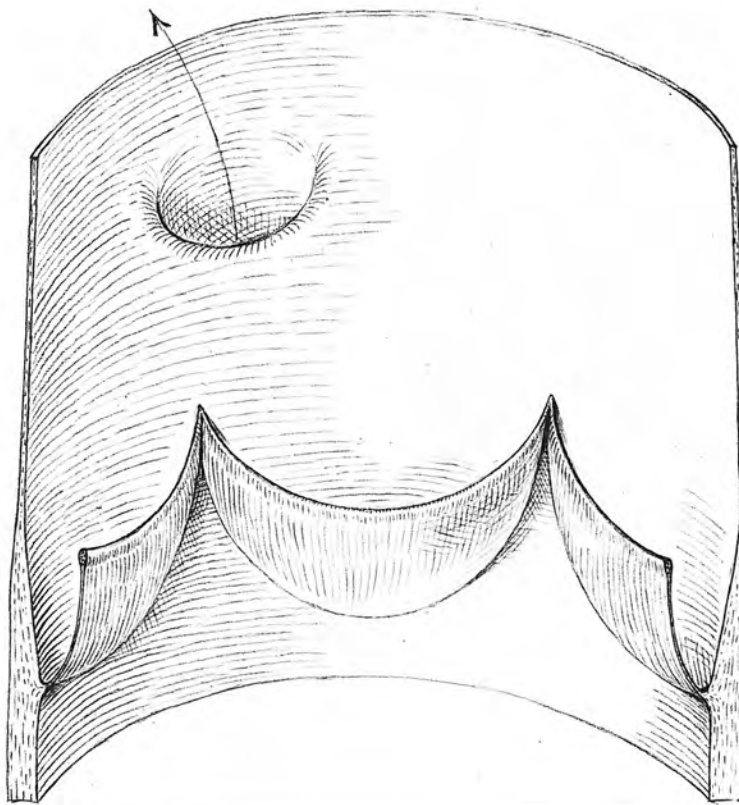


Fig. 52 . Interior of vein showing change in thickness of wall and the bicuspid valve.

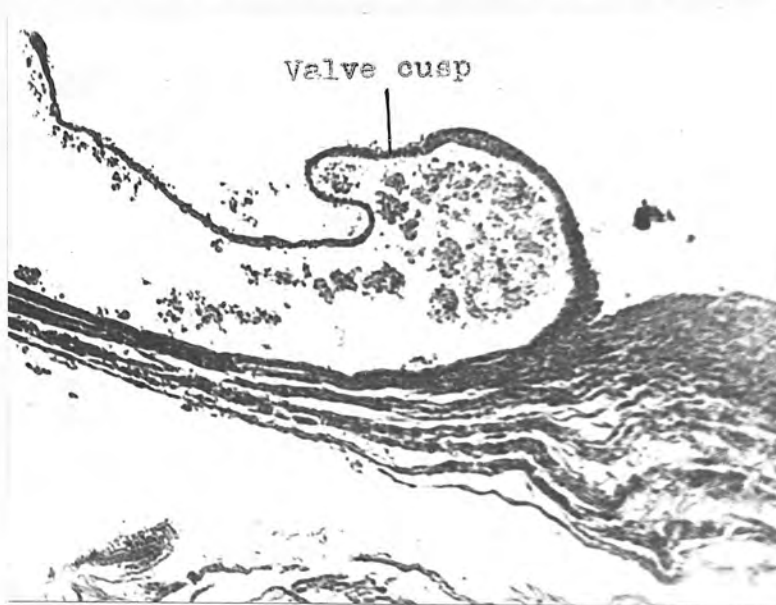


Fig. 53 . Photomicrograph of longitudinal section of vein showing change in thickness of wall and a cusp of the valve.

size of their lumen, show much variation in their thickness. Many of the superficial veins of the flipper and of the head have comparatively thick walls, but where those veins pass under some protecting structure - as within the thorax - their walls undergo a sudden diminution in thickness; in the region of the change there is a bicuspid valve (Fig. 52).

Some of the intestinal veins, e.g. anterior mesenteric, in both the adult and the foetus, have walls that are thicker than those of the corresponding arteries (Fig. 40). The increase of thickness in the vein walls is due to a hypertrophy of the tunica adventitia, and it is formed partly by fibrous and partly by elastic tissue.

Many of the veins have already been described with the arteries, and in this section the description of only the larger channels is given.

The anterior vena cava agrees in its formation and position with the usual condition where there has been a suppression of the left anterior cava.

It is formed behind the first costal cartilage 35 mm. to the right of the median plane by the union of the right and left innominates; it has a diameter of 13 mm. and its wall is comparatively thin. It has a total length of about 35 mm. and of this 20 mm. are extra-pericardial; the intra-pericardial part has already/



Fig. 54 . Photograph of heart and great vessels of foetus No. 1.



already been described (p. 29 ). It is covered on its superficial and lateral surfaces by the right thymus gland and medially it is related to the aorta and the innominate artery (Fig. 54).

Each innominate vein is formed ventral to the subclavian artery and just lateral to the vagus nerve by the union of the internal jugular vein, the costocervical vein, and the subclavian vein. The right innominate vein is 15 mm. long and 9 mm. wide and lies to the right of the innominate artery as it passes directly backwards to join the left vein. Between the two vessels there is a deep process of the left thymus and large cardiac branches of the vagus and sympathetic nerves. The left innominate vein is 70 mm. long and it passes almost transversely to the right to join the right vein; it is 10 mm. wide. It is covered on its ventral surface by the thymus glands and dorsally it rests on the branches of the aortic arch, and the laryngeal sac (p. 61 ).

Both veins receive tributaries from the thyroid gland and a large common trunk from the thymus gland opens into the left vein.

The internal jugular vein arises from the venous element of the intracranial rete and leaves the skull through the jugular foramen; at its emergence from the skull it has a diameter of 2 mm. It passes backwards/

backwards first on the rectus lateralis and then on the scalenus medius and is joined by the maxillary trunk under cover of the hyoid bone; in this part of its course it receives many tributaries directly from the muscles. The maxillary vein is formed by the veins accompanying the branches of the external carotid artery and tributaries from the pterygoid venous plexus. The internal jugular vein then proceeds directly backwards lying on the lateral side of the common carotid artery to join the other components of the innominate. At its termination the internal jugular has a diameter of 5 mm. and is not the capacious trunk as has been described by Schulte (1916).

The costo-cervical <sup>vein</sup> <sub>A</sub> lies on the lateral side of the costo-cervical artery and at its termination has a diameter of 6 mm. In addition to receiving tributaries which accompany the branches of the artery, its dorsal thoracic trunk receives the anterior termination of the spinal vein which is a large trunk that leaves the vertebral canal by passing through the first thoracic intervertebral foramen. The dorsal thoracic vein commences at the 6th intercostal space and receives the segmental trunks anterior to that level; it also has segmental communications with the spinal vein and receives numerous small vessels from the thoracic rete (see p. 148 ).

The/

The subclavian vein is formed by the union of the two axillary veins and a leash of vessels which pass backwards on the scalenus muscle. It lies ventral to the subclavian artery and receives the veins that accompany the branches of the artery except for the costo-cervical vein. Despite the large number of tributaries that join the subclavian vein it is only 4 mm. in diameter at its termination.

Although the main venous channels of the head, neck, and flippers are small, it is to be appreciated that the tissues of these parts are extremely vascular, and that there are numerous leashes of thin-walled veins in the supporting and subcutaneous tissues.

I was unable to discover any part of the azygos system in this specimen. The venous drainage of the six anterior intercostal spaces is through the dorsal and internal thoracic veins, and the posterior six spaces by the musculo-phrenic and spinal veins. The intercostal veins which enter the spinal veins are 3 mm. in diameter and they receive the dorsal segmental tributaries.

Ommanney (1932 a) has described a rudimentary azygos system in finback fetuses younger than my specimen, so that it is probable that the absence of the azygos veins is due to a progressive suppression of the right azygos venous line.

The/

The spinal veins are two longitudinal channels which extend from the anterior caudal region to the first thoracic intervertebral foramen through which they leave the vertebral canal to join the dorsal thoracic vein. They have a maximum width of 10 mm. and occupy an extra dural position ventral to the nerve roots; the right and left spinal veins are connected by frequent anastomatic channels. The anterior parts of the spinal veins are embedded in the spinal rete mirabile and many of the veins of the rete open into them. They are connected with the lumbar and dorsal thoracic veins by large spinal anastomosis and through these channels there is a free communication between the anterior and posterior cavae.

In the adult finback these vessels are relatively larger than they are in the foetus, and in the mid-thoracic region, where they are largest, they fill the greater part of the vertebral canal.

Schulte (1916) has associated the great development of the spinal veins with the suspension of thoracic respiration for long periods, the less favourable condition of the venous return depending upon the cessation of thoracic aspiration (see p. 175 ).

The posterior six intercostal veins also terminate in the spinal vein.

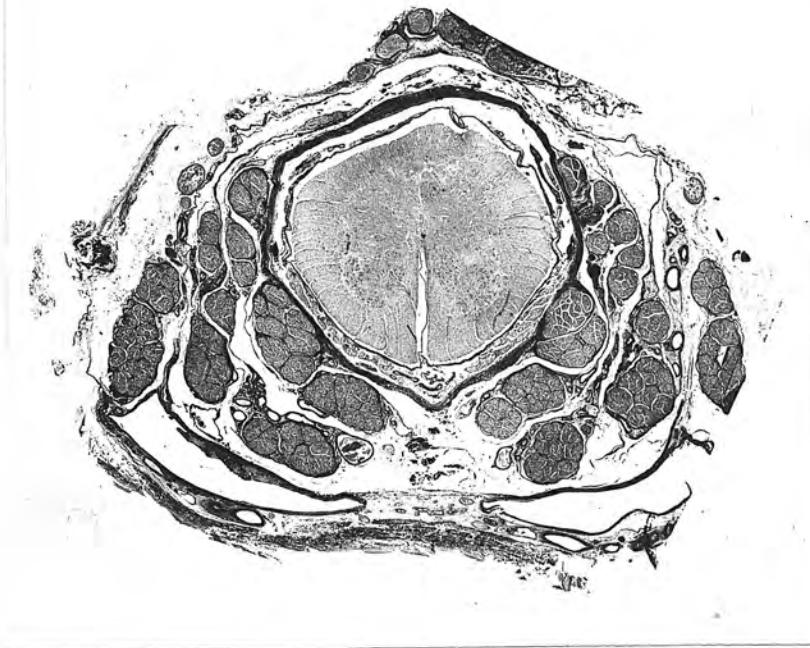


Fig. 55 . Transverse section of spinal cord, membranes and spinal veins at level of eighth thoracic vertebra. There is no spinal rete mirabile at this level but a few extra-dural vessels are seen among the nerves.



Posterior Venae Cavae. The posterior caval system is represented by right and left posterior cavae as far forwards as the left renal vein and anterior to that by a single ~~right~~ caval trunk (Fig. 56 ).

The right and left postcavae arise by the union of one of the caudal veins with a trunk that emerges from the pelvic venous plexus.

The pelvic plexus is composed of right and left parts each of which lies on the lateral side of the vagina and neck of the bladder; the common iliac artery and the proximal parts of its branches are surrounded by the plexus. The right and left halves of the plexus are continuous with each other through branches that pass ventral to the neck of the bladder and both dorsal and ventral to the terminal part of the aorta and the commencement of the caudal artery. The plexus is formed by (a) a branch from the caudal vein, (b) the superficial veins of the pedicle, and (c) the veins that accompany the branches of the iliac artery. Through the rectal veins of this last group an anastomosis between the systemic and portal circulations is established.

The posterior cavae continue forwards on the sides of the aorta, medial to the ureters, as far as the left renal vein. The left posterior cava unites with the left renal vein and the broad common trunk so formed/

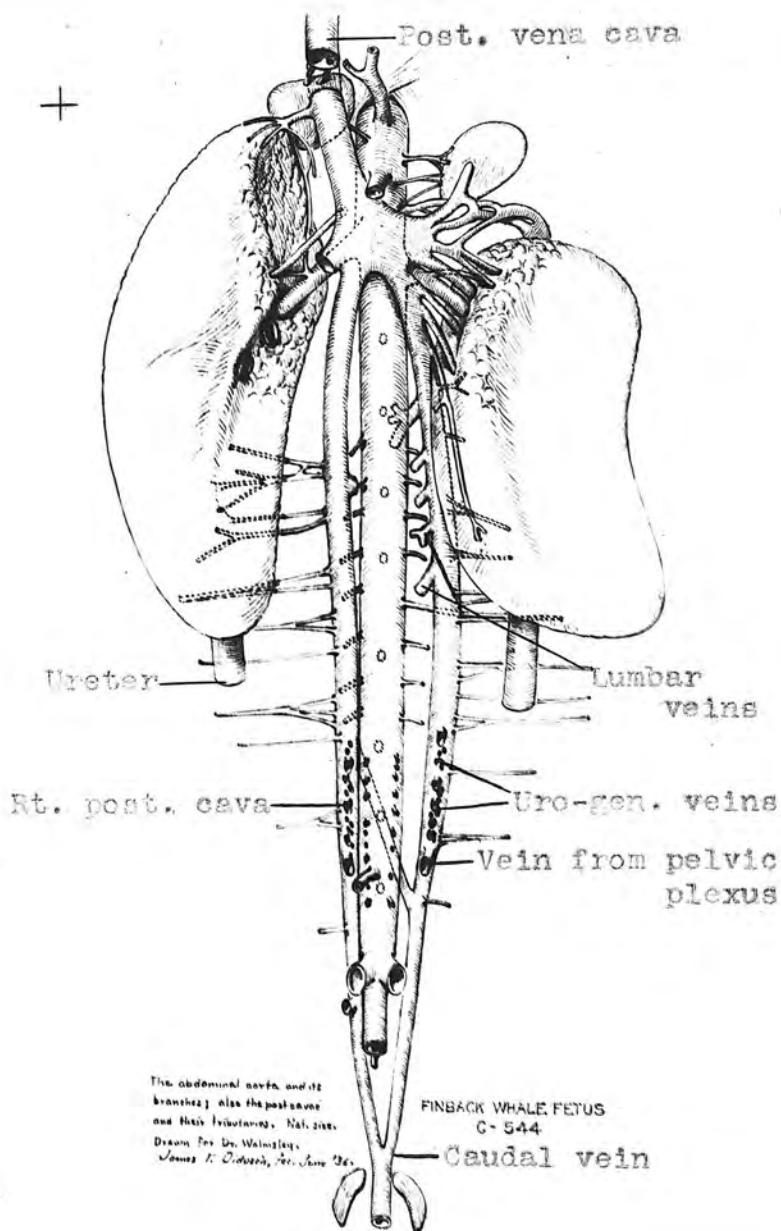


Fig. 56. The posterior venae cavae and their tributaries.

formed passes ventral to the aorta and unites with the right cava. This arrangement closely agrees with the condition in *Balaenoptera musculus* described by Daudt (1898) but differs from that described by Schulte (1916) for *Balaenoptera borealis* in which the left posterior cava joined the right through, a dorsal aortic anastomosis. In Schulte's specimen there were several dorsal anastomoses distal to the union of the right and left veins, whereas in my specimen there was only one such dorsal trunk which passed obliquely forwards and to the right between the distal parts of the cavae.

On account of the relationship of the cavae to the ureters and the presence of the dorsal anastomoses Slijper (1936) considers that the postcavae represent the supracardinal veins. This is in disagreement with the more general view that the double posterior cavae arise through the persistence of the posterior cardinal veins.

Tributaries.- In addition to the urogenital and renal tributaries which have already been described the posterior cavae also receive dorsal segmental vessels and small transverse vessels which emerge from the substance of the hypaxial muscle near its lateral border and pass medially on its ventral surface. These vessels are most numerous in the region of the kidney/

kidney with the superficial veins of which they are connected.

The dorsal segmental veins drain the abdominal and axial muscles and in addition have large spinal branches which join the spinal veins. The veins of the right and left sides form single trunks on the ventral surface of the vertebrae, and the posterior seven join the right cava and the anterior five the left cava (Fig. 56).

The subhepatic part of the right posterior cava is relatively narrow and lies on the right crus of the diaphragm and the adrenal gland; on its ventral surface there are the portal vein and the pancreas. In addition to two adrenal tributaries this part of the vein receives several segmental veins, among which there is a large spinal tributary. Proximal to the spinal tributary the vein shows a slight increase in width.

The hepatic segment of the vein is almost surrounded by liver substance; it receives one large and several small hepatic veins and the ductus venosus.

On its emergence from the liver substance the posterior cava pierces the diaphragm. Its intra-thoracic part is extremely short.

The portal vein is formed dorsal to the junction of the head and body of the pancreas by the union of the anterior mesenteric and gastro-splenic veins. The terminal part of the anterior mesenteric vein receives the pancreatico-duodenal and inferior mesenteric veins. These tributaries are all characterized by the thickness of their walls but the wall of the portal vein is of normal thickness. Dorsally the portal vein is in contact with the posterior cava - no peritoneum intervenes - and ventrally it is related to the bile duct and the small hepatic artery. In the porta hepatis it divides into two branches, the left of which is joined by the single umbilical vein and the ductus venosus. The umbilical vein is thin-walled and has a wide lumen; a little distal to the porta it is joined by an anastomatic vein from the epigastric venous plexus which lies in the substance of the rectus abdominis muscle. Through this anastomosis, as also through the vasa propria of the umbilical cord, there is a free communication between the umbilical and systemic veins.

The ductus venosus has a diameter of 3 mm. and passes to the hepatic part of the posterior vena cava in a deep fissure in the liver.



RETIA MIRABILIA AND CEREBRAL VESSELS.

It has already been noted that in this foetus there is an obliteration of the internal carotid artery during its course through the tympanic cavity, and also, that there is an absence of the vertebral arterial trunks. The functional loss or absence of these vessels is common to all Cetacea and it is associated with the development of a system of intra-cranial vascular channels, which if not entirely peculiar to Cetacea, are certainly most highly developed in them. As my findings have convinced me that the cerebral arteries are derived from the cranial extension of the spinal *retia mirabilia*, which in turn is a prolongation of the thoracic *retia mirabilia* I intend to commence this section of the work with an account of the last named structures. The major part of the intra-cranial venous drainage also has a course that is analogous to arteries.

The literature on the thoracic retia mirabilia in Cetacea is abundant and I shall do no more than make reference to some of the better known accounts.

The thoracic retia mirabilia are bilateral vascular masses which lie along the dorsal wall of the thorax and have a variable extension into the neck; the retia of the right and left sides are continuous with/

with each other ventral to the vertebral bodies.

Extension of the right and left retia into the vertebral canal is generally recognised, but the farther extension of the retial tissue into the cranium has been described by but a few workers, viz.- Mackay (1886), Boenninghaus (1903) and Slijper (1936).

The actual structure of the retial mass, that is whether it is composed of arteries, veins, or capillaries or a combination of two or three of them, is still as open a question as when Hunter described the tissue - 150 years ago. Hunter (1787), Breschet (1836), Stannius (1849), Barkow (1866), Turner (1870) and Bouvier (1889) etc., all maintain that the retia are arterial in structure. Murie (1874), Wilson (1879) and Slijper (1936), however, state that the retia are formed of both arteries and veins. Ommanney (1932 a) in his summary of the retial tissue states: "The rete is everywhere in free communication with the vessels it surrounds, whether arteries or veins. It does not, however, block the course of any of them. This is opposed to the earlier conception of the retia, according to which these networks were supposed to be formed on the course of either an artery or a vein. The foregoing description shows that they must be looked upon as capillary systems intervening between arteries and veins".

As far as I am aware no account of the microscopical anatomy of these structures has as yet been given.

In the foetus the thoracic rete mirabile was less prominent than I had been led to expect from the accounts of it. It is a rather soft, spongy, elongated body of pink colour which extends along the bodies of the first five thoracic vertebrae and into the foraminae transversariae of the cervical vertebrae. In the thoracic region its greatest mass lies in the angle between the ventral surface of the transverse processes and the side of the vertebral bodies, but it extends along the whole length of the first rib and first intercostal space. Medially it extends (a) ventral to the vertebral bodies to become continuous with the rete of the other side, and (b) through the intervertebral foraminae to become continuous with the spinal rete, which is in reality, a continuation of the two retia. Each rete lies without the parietal pleura and has the typical vascular relationship to the endothoracic fascia which provides it with a thin fibrous capsule. The dorsal thoracic artery and vein are in relation to its lateral edge and their dorsal trunks pass through the substance of the rete as shown in figure 57. As the spinal nerves emerge from the intervertebral foraminae they penetrate the retial substance/

Semi-schematic section at level of 3<sup>rd</sup> thoracic vertebra  
 of adult Finback whale to demonstrate the continuity  
 of the thoracic rete mirabile and the spinal rete mirabile.  $\times \frac{1}{2}$   
 Vertebra from whale skeleton #236,690 in the collection of  
 National Museum, Wash. D.C. Drawn for Dr. Walmsley  
*James F. Bridwood, Fleet. Nov. 1936.*

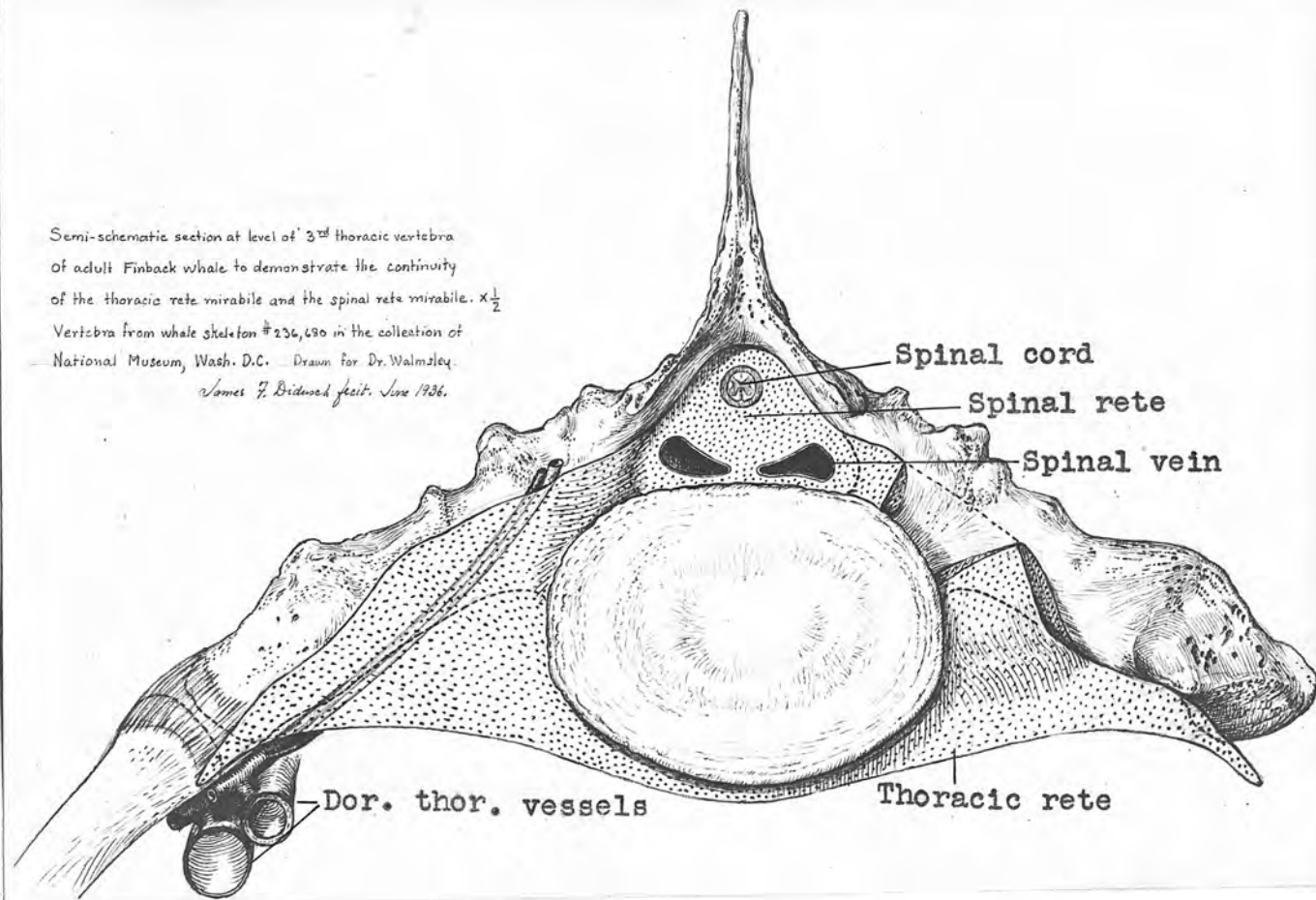


Fig. 57. Schematic section of retia mirabilia at level of third thoracic vertebra. The stippled area represents the retia. The dorsal thoracic vessels lie near its lateral edge, and the spinal veins are embedded in the spinal rete. The diagram is based on a third thoracic vertebra of an adult finback loaned by the National Museum, Washington, D.C., U.S.A.

substance and they are accompanied in this part of their course by the spinal veins and arteries.

As the dorsal thoracic artery passes backwards in relation to the lateral edge of the rete, and as its dorsal branches pass through its substance, numerous small twigs are given off and enter the rete. These twigs are so numerous and small and have such a tortuous course in the rete that no appreciation of their ultimate destination could be obtained by either macroscopic or microscopic dissection. In a similar way, small veins, plentiful but not so numerous as the arteries, pass from the rete into the tributaries of the dorsal thoracic vein. From these observations, however, it was established that there are both arteries and veins in the thoracic rete mirabile.

On microscopical examination the thoracic rete mirabile and its cervical extension is seen to be composed of both arteries and veins embedded in loose areolar tissue, and the vessels are so intermingled that they form a true arterio-venous plexus (Fig. 59 ). Though the arteries have frequent anastomoses among themselves and the veins likewise, I was unable to discover any evidence of arterio-venous anastomoses. The arteries show a certain amount of variation in calibre (Wilson, 1879), but there is no indication of a generalized capillary formation as is described by/



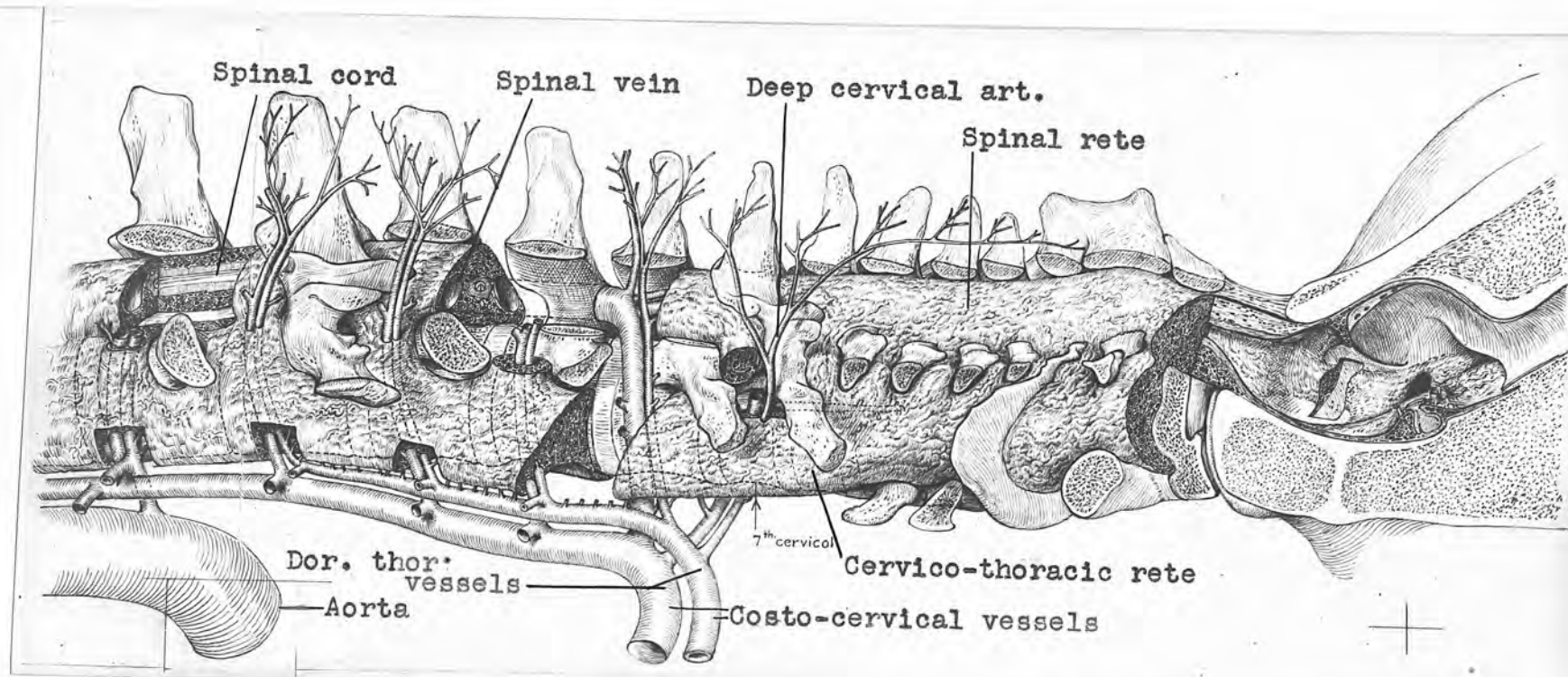


Fig. 58. Composite diagram of the retia mirabilia. Parts of the vertebrae and the skull have been removed to show the continuity of the various retia. This diagram is based on part of a skeleton of an adult finback whale, loaned by the National Museum, Washington, D.C., U.S.A.

by Ommanney (1932a). The thickness and structure of the walls of the arteries are typical for vessels of their size.

The veins of the rete have extremely thin walls and in this respect they agree closely with the spinal and intra-cranial veins. The veins are most numerous in the region of the intervertebral foraminae, and are almost absent in the most ventral part of the rete.

The spinal rete mirabile extends from the level of the mid-thoracic region to the foramen magnum through which it becomes continuous with the intra-cranial rete. It is extra-dural in position and its main mass lies ventral to the spinal cord. It may be taken to represent, and to be an excessive development of the extra-dural spinal meningeal system. The general structure of the rete is similar to that of the cervico-thoracic rete with which, as already stated, it is continuous; the vessels composing it, however, are of a smaller calibre.

The cranial rete mirabile is directly continuous with the spinal rete through the foramen magnum. From the foramen magnum the vessels of the right and left sides sweep around the base and side wall of the skull and pass medially to the body of the sphenoid on which they form a vascular mass in which the hypophysis is embedded. The structure of the retial tissue in the region/



Fig. 59 . Section of thoracic rete mirabile from foetus No. 1. This specimen was taken from between the first and second transverse processes and shows arteries and veins.



Fig. 60 . Section of spinal rete mirabile from foetus No. 1. This specimen was taken from the spinal rete at the level of the fourth cervical vertebra.

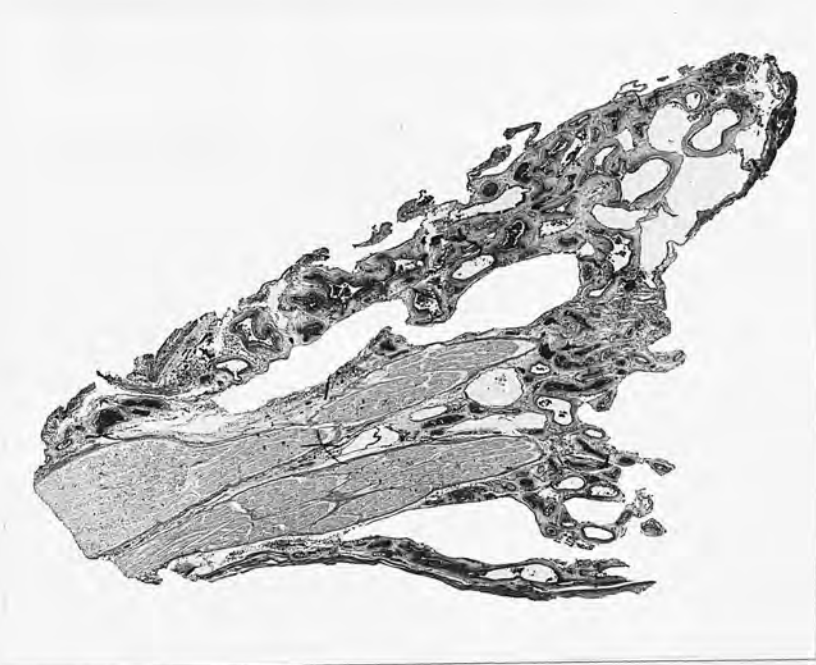


Fig. 61 . Spinal rete mirabile and roots of sixth cervical nerve of foetus No. 1.



Fig. 62 . Cranial rete from the side of the body of the sphenoid of foetus No. 1. The vein (or venous sinus) is indicated by a "V".



region of the sphenoid is similar to that of the other retia and is shown in figure 62 . A process of retial tissue surrounds the optic nerve and passes through the optic foramen. The cranial rete lies in <sup>the</sup> <sub>A</sub> same plane as the cranial venous sinuses and the spinal rete, i.e., between the dura mater proper, and the internal periosteum of the cranial bones. This rete has been referred to by other authors as the rete arteria carotis and the rete mirabile cerebri.

Owing to the complete decomposition of the brain, I was unable to make further observations on this system in the foetus and the following account is based partly on observations on preserved material and partly on fresh material at Rose Harbour, Queen Charlotte Is., British Columbia.

The thoracic rete mirabile in fresh adult whales forms great vascular masses along the dorsal thoracic wall. Like the other parts of the retial system the thoracic rete is relatively very much larger in the adult than in the foetus, and to one who has limited his studies to the foetus this is the most arresting difference to be noted. The retial material is bright red in colour; it is formed of vessels which have an average diameter of about 4 mm. and are embedded in a loose fatty tissue. Measurements of the tissue in situ would be of little worth for it is soft/





Fig. 63 . Photomicrograph of section of thoracic rete mirabile of adult finback whale. There are only arteries in this field.

soft and without a strong limiting membrane and thus alters much in form in the opened thorax.

The rete, however, it was noted, extends along the inner surface of the first rib and intercostal space. It is evident, however, even to gross examination, that the retial tissue is much more abundant in the sperm whale (*Physeter macrocephalus*) than in the finback whales; the significance of this is considered in the discussion.

On microscopical examination the rete is seen to be composed of arteries and veins and both have numerous anastomoses among themselves; the arteries are more numerous and have a larger calibre than the veins.

The spinal rete has a similar appearance and structure to the thoracic rete, but on microscopical examination the veins in it are seen to be relatively larger and more numerous. In the cervical region the rete fills the entire extra-dural part of the vertebral canal. In the finback it extends as far back as the mid-thoracic region closely surrounding the dura mater and the spinal veins, but in the sperm whales it reaches as far caudally as the anterior lumbar region. Many of the veins in the rete open directly into the spinal veins and this accounts for the relatively greater number of veins in the spinal than in the thoracic rete.

The/

The size and extension of the spinal rete in the adult are much greater than the foetus, where the rete is poorly developed and occupies only a part of the extra-dural space in the cervical region. In the adult the appearance of this mass and its relations to the spinal cord and dura mater can be best appreciated by the removal of a part of it and fixing it in formalin; a section of this is shown in figure 64. In this specimen, which is from the cervical region of an adult finback, the rete is 150 mm. transversely and 80 mm. ventro-dorsally, whereas the spinal cord has a diameter of only 13 mm. With a magnification of X 4 (Fig. 64) the structure of it is easily recognised; the veins have extremely thin walls and their lumina are occluded so that they are not so easily recognised as the arteries, and this may account for the rete so often having been described to be formed only of arteries.

In the anterior part of the vertebral canal the rete lies entirely ventral to the spinal cord and as it passes through the foramen magnum it divides into right and left halves. Each half passes forwards and laterally on the side wall of the skull as a wide vascular lamina, which lies between the dura mater proper and the periosteum and has an average thickness of 13 mm. Each sweeps medially to the body of the sphenoid/

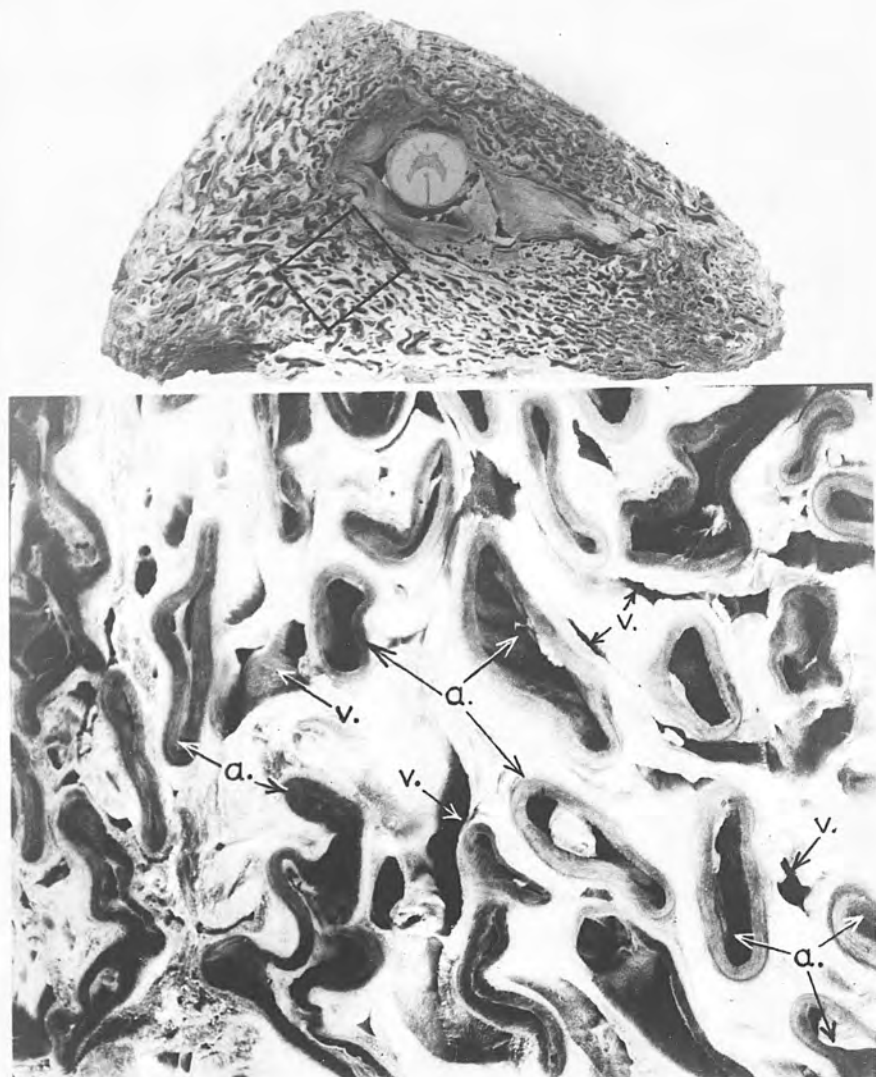


Fig. 64 . The upper photograph represents a transverse section of the cervical part of the spinal cord and the spinal rete of an adult finback whale (X.7).

The lower photomicrograph is the bracketed area of the upper X4. The arteries and the thin-walled veins are indicated by arrows.

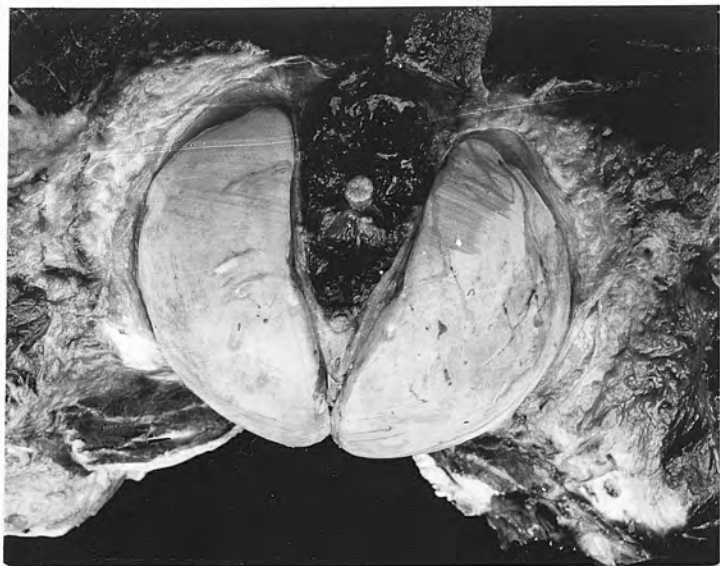


Fig. 65 . Photograph of the condylar region of the skull of an adult finback whale. The spinal cord is embedded in retial tissue.



Fig. 66 . Photomicrograph of section of cranial rete from region where cerebral arteries arise.



sphenoid on which the two sides join together and form a vascular mass 60 mm. thick and in which the hypophysis is embedded. No vessels pass directly forward on the basi-occipital or basi-sphenoid bones, on which the dura mater is about 5 mm. thick and avascular. The structure of the intra-cranial (cerebral) rete is essentially similar in all its parts, as has been verified by numerous sections, and it is formed of rather thin-walled arteries and extremely thin-walled veins (Fig. 66 ). In the region of the hypophysis, however, the vessels are rather smaller and are very tortuous, whereas on the side wall of the skull the vessels have a general antero-posterior direction and are not so tortuous; in that region the larger vessels have a diameter of about 7 mm. The change from the one form to the other is sudden and takes place about 80 mm. from the median plane.

About 35 mm. from the median plane, and in the same coronal plane as the infundibulum, many of the arteries of the rete join together (Fig. 67 ) in the same way as the roots of a tree join the main trunk, and form a cerebral artery which has a diameter of 6 mm. This artery pierces the dura mater (i.e. the dura mater proper) and passes laterally to the root of the lateral cerebral sulcus where it divides into an anterior and a middle cerebral artery; the anterior/

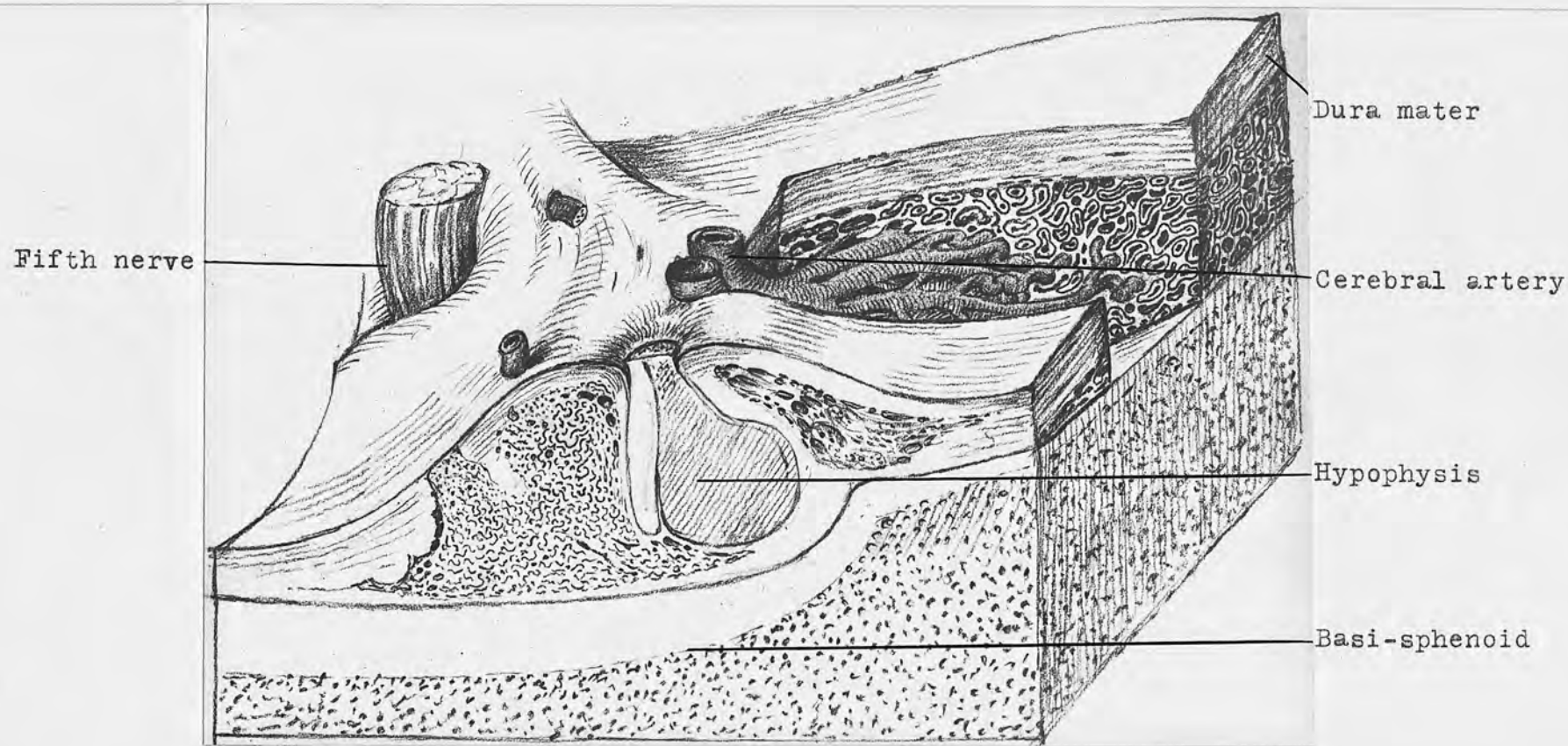


Fig. 67. Diagram showing the mode of origin of the cerebral artery. The diagram is a median section through the body of the sphenoid, the hypophysis and the surrounding retial tissue.

anterior artery has a diameter of 3 mm. and the middle artery has a diameter of 4 mm. A posterior cerebral artery arises from the rete about 30 mm. behind the main arterial trunk. The three cerebral arteries have a course and distribution similar to the typical mammalian stems, although more collateral trunks than is customary arise from them. A small superior cerebellar artery also arose from the posterior part of the rete. The optic nerve is accompanied through the optic foramen by a prolongation of the retial tissue.

In the posterior ramus of the lateral sulcus there is a complex network of superficial and deep cerebral veins which surround the branches of the middle cerebral artery; they form a single trunk which enters the rete close to the origin of the main cerebral artery. Most of the veins of the supero-lateral surface of the brain drain into these cerebral veins; and only a few of the dorsal veins enter the superior sagittal sinus which is represented by several small channels in the dorsal part of the falx cerebri. I was unable to demonstrate the termination of the anterior cerebral veins.

The great cerebral vein is formed ventral to the splenium of the corpus callosum by the union of two internal cerebral veins. The great cerebral vein is/

is about 30 mm. long and terminates in the junction of the falx cerebri and the tentorium cerebelli. It also drains a dense venous plexus which surrounds the mid-brain and extends onto the dorsal surface of the cerebellum.

The material I had access to only allowed me to make very imperfect examinations of the veins of the brain as the brains were decomposing by the time I had opened the cranial cavities. By the examination of the membranes however, I satisfied myself that no large venous channel passes out through the jugular foramen and that the main route of venous drainage is through the venous element of the spinal rete.

In summarizing this section it can be said that the cerebral arteries arise from the intra-cranial rete mirabile. This rete is the direct continuation of the spinal rete which in turn is a prolongation of the cervico-thoracic retia, the continuity being effected by processes of retial tissue which pass through the intervertebral foramina. The arterial part of cervico-thoracic rete is derived from the dorsal thoracic artery and its branches.

The principal route of intracranial venous drainage is through the venous element of the spinal rete, many of the veins passing directly into the large spinal veins, others entering the dorsal thoracic vein and/

and its tributaries.

As has been already stated, the spinal rete is homologous with the extra-dural spinal meningeal system. This rete, as also the cranial rete mirabile (rete arteria carotis, rete mirabile cerebri), is also present in most of the Artiodactyla, and the retia of the ox, as I have verified by microscopic section, have a structure similar to those of the Cetacea. They do not, however, form the large vascular masses which are characteristic of the Cetacea, but they are limited to a relatively small plexus that lies in the cranium and the anterior part of the vertebral canal; in the ox the vascular supply of the brain is derived mainly from the cranial rete. In the Artiodactyla the arterial component of the system is formed by vessels (vertebral, occipital and maxillary) which in some part of their course lie outside the bony protection of the axial skeleton, and in this respect the origins of the retia in the Artiodactyla and Cetacea differ. In the Cetacea the arteries which are destined for the brain are afforded the maximum possible protection by the axial skeleton, for as they lie in the retia they are successively within the thoracic cavity, the vertebral canal and the cranium; as they pass from the thorax into the vertebral canal through the intervertebral foramina they are covered by/



by the thick hypaxial muscles. I therefore regard the **course** of the cerebral vessels as one of the adaptations of the Cetacea to the large external pressures to which they are subject during deep submergence.

DISCUSSION.

I assumed before I commenced my dissections that the peculiarities of the vascular system of whales would be adaptations to the unusual conditions determined by the habit of submergence; and, as far as I am able to state them, the unusual conditions are (1) the greatly prolonged intervals between respirations, or, as I prefer to name them, phases of respirations, and (2) the increased pressure on the surface of the body when submerged. There are, however, very great differences in the recorded observations of the whales respiration and the depths they descend to in diving, and, as the facts are of some importance, I propose to record the observations I made during an expedition in the North Pacific from the Rose Harbour Whaling Station on the Queen Charlotte Islands.

Whales live for the most part in the high seas, seldom passing into shoal water except in difficulties. They migrate each year from arctic to tropical waters. The temperature of the arctic waters is  $4^{\circ}\text{C}$  or less, and of the tropical waters  $25^{\circ}\text{C}$  or more. The body temperature of the whale has been given as  $31.1^{\circ}$ ,  $36.6^{\circ}$  and  $36.9^{\circ}\text{C}$ , that is, a little lower than that of the horse ( $38.2^{\circ}$ ) and the sheep ( $40.2^{\circ}$ ). As there are/

c/-  
c/-

are no sweat glands in whales, the body temperature must be regulated by the altered activity of the blood vessels of the skin and/or by the control of the basal metabolic rate. The blubber, however, it is generally held, is a protection against the cold of the arctic waters.

The length of the time of submergences varies in the different species of whales. In the finback whale (*Balaenoptera physalus*) the average normal time of submergence is from 7 minutes to 10 minutes, but in the sperm whale (*Physeter macrocephalus*) it is, on an average, 30 minutes but may be up to 45 minutes or even 50 minutes. These figures closely agree with several other records, and for the purpose of calculation I have taken 10 minutes for the finback and 30 minutes for the sperm whale as the normal times; a wounded whale, it is agreed, may remain submerged for times twice as long as the normal times.

The consequence of such prolonged intervals between phases of respiration has been very generally accepted to be a suspension, or partial suspension, of the oxygenation of the blood, and, therefore, the tendency for there to be a shortage of oxygen and an accumulation of carbon dioxide at the end of submergence. This view and the corollary that the retia mirabilia form "reservoirs of oxygenated blood which re-enters/

re-enters the circulation during submergence" is thus expressed by Mackay (1886): "The generally accepted explanation of the use of these great retia is that they act as stores for oxygenated blood which is brought into use while the animal remains for a long time underneath the water..... The spinal cord, supplied by a rete,--- would thus receive pure blood, while the brain would get its supply through the posterior cerebral artery from the spinal rete". It is with interest that I noted that John Hunter (1787) after his description that "the medulla spinalis is surrounded by a network of arteries --- more especially where it comes from the brain, where a thick substance is formed by their ramifications and convolutions" says "The motion of the blood in such cases must be very slow; the use of which we do not readily see".

It seems to have been conclusively shown by Laurie (1933), however, that there is no likelihood of an oxygen shortage in normal submergence, and as his findings are of much interest I add a summary of them.

The/

The definition of the basal metabolic rate by Starling is: "We may say that a warm blooded animal requires a daily expenditure of 1000 cal. per sq. met. of body surface to carry out the motor processes essential to life". The surface area being less in proportion to body weight in large than in small animals the metabolic rate in whales may be expected to be low; more especially when there is reason to suppose that they are not active when submerged. The calculated rates given are:-

Guinea pig:	223.1 cal. per kg. per day
Rabbit :	58.5 " " " " "
Man :	32.9 " " " " "
Whale :	2.25 " " " " "

On these calculations a man requires 4.28 c.c. of  $O_2$  per kg. per min. and a whale's requirements will be 0.293 c.c. of  $O_2$  per kg. per min.; and for a whale of 160 tons this represents a requirement of 35.75 litres of  $O_2$  per min. or 178.75 litres of air. It was calculated from measurements of the thoracic cavity, the necessary allowances seeming to be made, that the vital capacity of a whale 160 tons in weight is 3050 litres; so that assuming all the  $O_2$  in the lungs is utilised, and that there is no muscle exertion, the possible time of submergence is 17 mins.

Laurie's work was done on the blue (*Balaenoptera musculus*) and the finback whale.

I have concluded, therefore, that the possibility of oxygen shortage is not to be considered a determining factor of the structure and arrangement of the vascular system.

It is generally considered that the amount of blood in whales is proportionately greater than in land mammals; according to Laurie (1933) the volume of blood in the blue whale is 6.6% of the total weight while the blood volume in man is 4.9% of the body weight. There is, however, a smaller content of haemoglobin/



haemoglobin in the blood of the whale, the amount in the blue whale being 9.6% as compared with 13.8% in Man. There is, therefore, a relatively smaller capacity for the storage of oxygen in the whale than in Man, a matter of great disadvantage if there was a tendency to oxygen shortage during submergence; that the facts are as they are seems to me also to show that there is no such shortage to be considered.

The respiratory habits of the whale may themselves, however, influence the pattern of the vascular system. My own observations are that after a full submergence, 7 - 10 minutes in a finback whale and 30 minutes in a sperm whale, the head of the whale appears above the surface and the whale expires; no attempt is made to start expiration until the water surface has been broken. The blast of expiration is visibly represented by the "spout", the noise of which is audible for as much as half a mile on a still day; it is obvious that expiration is extremely forcible and the expiratory effort is very great in the rapid passage of a large volume of air through the blow-holes. Expiration, which lasts about 1 second, is immediately succeeded by inspiration; it lasts about 1 second and is sometimes audible as the air rushes into the lungs. After inspiration is completed the head submerges and the hinder part of the body appears on the surface as though/

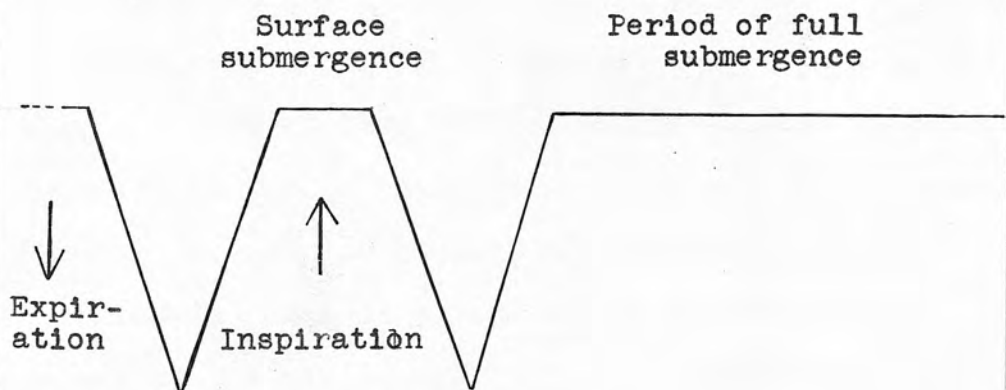
though the whale was weighted down by the head in front and raised by the distended lungs behind and moving round a transverse axis near the middle of the body; the whale travels at a speed of about 7 knots, as nearly as I was able to judge from the speed of our ship, during these acts. The body itself appears above the surface for about 4 seconds, after which the flukes appear, sometimes high in the air, and the whale submerges. This submergence, however, is shallow, and in a variable time usually about 15 secs., the head again appears and the respiratory act is repeated. The number of respiratory acts so repeated after a full submergence is fairly constant for each species, and, in my observation, about 10 in number for the finback whale and 40 in number for the sperm whale; that is they are directly proportional to the time of full submergence. This series of respirations I refer to as the "respiratory phase".

The large amounts of air which enter the lungs during a respiratory phase must allow the blood to be thoroughly oxygenated, and, as already stated, the vital capacity is sufficient for the needs of a full submergence. The sequences of the parts of the respiratory act, however, is opposite to the sequence in land mammals. In land mammals the normal tracing of the contraction of the diaphragm, and presumably of/

of the abdominal muscles in respiration is as follows:-



In the whale, however, the normal tracing must be approximately as follows:-



The whale thus submerges with the inspiratory act at its full development and the inspiratory muscles fully contracted and during the forcible expiration there must be a sudden relaxation of them.

The submergence of whales is normally for the purposes of feeding and since the food sought occurs between the surface and a depth of 100 metres, the lower limit of normal activity may be taken as such;  
whales/

whales also submerge for protection when wounded and it is probable that they then descend to much greater depths. The direct effect of submergence is an increase of pressure on the body surface, the increase being 1 atmosphere, or 14 lbs. to the square inch, for each 10 metres of depth; at 100 metres depth the total pressure is 11 atmospheres or 154 lbs. per square inch. This pressure bears equally on the whole surface of the body and as the body surface even with the layer of blubber cannot be considered unyielding, uniformly compresses the internal organs not contained in bony cavities. The air in the lungs is compressed 10 times at a depth of 100 metres; the oxygen is then at a pressure of 1500 mm. Hg. and as a pressure of 60 mm. Hg. is sufficient to keep the blood 80% saturated the fullest use can be made of the oxygen.

The increase of pressure will diminish the volume of the air in the lungs, and, omitting changes in temperature, 10 vols. at 1 atmosphere pressure is reduced to 1 vol. at 11 atmospheres pressure; with a decrease in temperature there is a slightly greater reduction. This large decrease in the volume of the contained air must be accompanied by a considerable diminution of the volume of the lungs, and this probably explains the large amount of elastic tissue in the thick inter-alveolar walls of the lungs of whales/.

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whales. The lungs must be subject, therefore, to considerable changes in size; while the whale is at the surface they are fully expanded and while it is submerged they are compressed. This difference in volume is probably also a factor in the diminution of the thoracic skeleton and the forward extension of the abdomen ventral to the thorax, the abdominal contents being used to assist in filling the potential thoracic space in submergence.

I have considered, therefore, that the peculiarities of the vascular system of whales will not be provisions for a possible shortage of oxygen, for a shortage does not occur, but will be adaptations to the differences of pressure under which their habits compel them to live.

In the section on the retia mirabilia it was stated that the intra-skeletal course of the cerebral vessels is regarded as an adaptation to marine life. Further, I conceive that the very presence of the thoracic retia and their distribution in the thorax are largely dependent on the diminution in lung volume that occurs during submergence, as the retia will then become engorged and will occupy the interval which would otherwise be created within the non-collapsible part of the thoracic cavity; and this explanation seems to me also to include the fact that the retia extend around the thoracic wall only on those ribs which/



which are directly connected to the sternum. As the retia form the afferent supply of the vascular masses which are distributed to the central nervous system, there is thus ensured for that system, not only a continuous supply, but one which is even more certain the deeper or more prolonged the submergence.

This explanation implies that when the lungs expand as the whale comes toward the surface and during the respiratory phase, the thoracic retia will lose much of their blood. The depletion is almost entirely positive, that is, it is brought about by a lessened arterial supply, there being, as I stated in my description of the cervico-thoracic retia, but little venous tissue in them.

In the whales that I have had the opportunity of examining, I have noted that the retia mirabilia are relatively the largest in those species which can remain sub-merged for the longest time.

The ductus venosus has been described by Knox (1838), Murie (1865), Turner (1870) and others as being patent in adult whales and it has been suggested that when there is a collapse of the lung, blood may pass from the pulmonary circulation to the systemic circulation through the ductus. Pohlmann (1924) and van Gelderen (1928), however, maintain that when an open ductus is associated with a closed foramen ovale, no/

no blood passes along the ductus.

When the whale comes to the surface, and the thoracic retia are almost depleted of blood, there must not be a respiratory depletion of the intra-spinal and intra-cranial retia. The mechanism on the internal jugular vein in Man to prevent the respiratory depletion of the intra-cranial venous system is well known; the mechanism in the Cetacea seems to me as follows: In the spinal and cranial retia the arterial and venous contents are about equal. These relatively large venous fields I have described to be drained chiefly by the spinal veins, and the spinal veins in turn to drain anteriorly into the dorsal thoracic component of the innominate vein but posteriorly into the post-hepatic segment of the posterior cava. The posterior connection ensures that the thoracic inspiratory suction, which might effect at least a partial depletion through the anterior connection, is at least not active over the whole system and may even be negatived by the rise in intra-abdominal pressure.

There are two further peculiarities of the vascular system<sup>to</sup> which I wish to make reference:-

(1) I have described the genito-urinary viscera as being supplied with multiple arterial stems.

These/

These multiple stems would ensure to a very greatly enlarged pregnant uterus a sufficiency of single stems for the supply of the capillary field\*.

It may also well be that the powerful movements of the posterior part of the body may so possibly affect the pelvic viscera that multiple stems are necessary to avoid the possible temporary compression of a single large stem.

The latter causative factor, i.e. the effect of a large range of movement, may also be the explanation of the multiple condition of the inferior dental artery.

Apart from these specific instances, where, in my opinion, the causation of the arterial multiplicity is to be sought in extra-vascular factors, I wish to draw attention to a generalized arterial state of which I have described examples in the coronary and cerebral arteries, namely the breaking up of what in human anatomy is a single trunk into collateral vessels. This state, it seems to me, is an evidence of a generally accepted conclusion, that the blood pressure in Cetacea is low; with the low blood pressure there is to be associated the relatively large amount of total blood to which I have already referred.

(2)/

finback

\* The average length of a full-time <sup>A</sup> foetus is about 20 feet.

(2) The intra-pericardial parts of the pulmonary artery and its branches, the ascending aorta, the aortic arch and its branches, and the ductus arteriosus are characterized, I have stated, by their extremely thick walls; this condition of thick-walls does not extend to the coronary arteries. The thickness of the arterial walls is relatively much greater in the foetus than in the adult, but even in the adult the aorta is extremely thick and has frequently been so described; a specimen of the ascending aorta of an adult finback whale which I measured was 51 mm. thick. I have been especially impressed with what has not been previously commented on, namely that the great thickness of the arterial walls is confined to their intra-pericardial parts, and the explanation which I put forward for this thickness does not explain this fact.\*

It is well established that with an increase in body size there is a proportionate increase in the transverse section of the proximal aorta and therefore with the thickness of the aorta wall. This relationship serves to explain the large size of the following measurements I made on fresh adult finback whales.

\* I hope at some future time to make an examination of the thickness of the walls of the intra-pericardial and extra-pericardial parts of the aorta and the pulmonary artery in more easily investigated species.

Species	Sex	Length	AORTA		PUL. ART.	
			Thick- ness	Diam- eter	Thick- ness	Diam- eter
Finback	Fem.	49ft.	35mm.	220mm.	25mm.	200mm.
Finback	Fem.	58ft.	51mm.	300mm.	30mm.	200mm.

It is possible, however, that the thickness of the wall also increases relatively to the heart rate but I have no data on this matter; my assumption is that in the performance of its function in receiving a considerable amount of the work of the heart and maintaining an even flow of the blood stream from it, the amount of elastic tissue in the aorta and pulmonary artery would be increased with an increasing interval between the heart beats.

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SUMMARY.

A systematic description is given of the vascular system of a female foetal finback, 1430 mm. long. This is supplemented by histological accounts of many of the tissues. The heart and the retia mirabilia have been more fully described than the other parts. The retia are relatively much larger in the adult than they are in the foetus, and therefore a description of the retial system as observed in adult sperm and finback whales has been added. In the discussion the functional significance of the retia mirabilia, the multiple arterial stems and the thick-walled aorta and pulmonary artery has been considered. In summing up the peculiarities of the vascular system in the Cetacea, it may be said, that they are not provisions for a possible shortage of oxygen, for a shortage does not occur, but that they are adaptations to the differences of pressure under which their habits compel them to live.

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